EVIDENCE EXCLUDING MUTATIONS, POLYSOMY, AND POLYPLOIDY AS POSSIBLE CAUSES OF NON-MENDELIAN SEGREGATIONS IN SACCHAROMYCES[1]

BALAJI D. MUNDKUR[2]

Tetrad analysis, the direct genetical characterization of the segregation products of meiosis, has frequently revealed the occurrence of ratios differing from the 1:1 gametic segregations implicit in the postulates of classical Mendelian genetics. Although many of these exceptions to regular segregation have been reported in the fungi, which offer advantages for genetical analysis denied to the geneticist studying higher organisms, the bases for inferring such divergent segregations were not beyond criticism. Previous workers using the fungi as genetic material investigated inadequately marked stocks (generally only one marker was used) and the deduction of truly non-Mendelian ratios was therefore rendered ambiguous by the possible occurrences of chromosomal aberrations. The few markers used were not sufficient to establish hybridity of the stocks analyzed, and, usually being morphological, introduced obvious difficulties in diagnosing the segregants with accuracy. The occurrence of mutations in the segregants during vegetative growth prior to diagnosis was not excluded as a possible cause obscuring an initially Mendelian segregation.

The experiments reported in this paper were designed with the above considerations in view and present data eliminating the questionable features involved in evaluating non-Mendelian inheritance. In the tetrad analyses of the five hybrids

of phenotypes, and mutants of non-fermenter haplophase segregants *(g* or *me)* to fermenter phenotypes *(G* or *ME)* produced in genetically unstable lines should have equal opportunities for growth. When a hybrid ascus heterozygous for *G/g* and *ME/me* is dissected, one expects two ascospores to be non-fermenters. However, if mutation occurred on glucose after these two spores germinated, each segregant culture would comprise mixtures of original *g* and mutant *G* clones. When this mixed population is used as inoculum in testing for galactose (or melibiose) fermentation the mutant cells would be selected and would achieve fermentation. A highly mutable *(g* to *G; me* to *ME)* haplophase segregant is thus apt to be diagnosed as an extra-fermenter although the ascospore giving rise to the mutant clones was genotypically *g* or *me* when isolated from the ascus.

Similarly, loss mutations *(G* to *g; ME* to *me)* are apt to yield fewer than the expected number (two) of fermenter phenotypes when mature glucose-grown clones are tested for fermentation.

Situations such as these could obscure Mendelian segregations and lead to the incorrect conclusion that gene transformation had occurred. Originally *G G g g* spore tetrads (where either allele is highly mutable) might be finally diagnosed as *G G G G, G G G g, G g g g,* or *g g g g.*

A helpful criterion for determining whether the non-Mendelian segregations are cases of gene conversions or of mutations during growth on glucose would be, of course, the abilities of the four segregants to ferment at the earliest stage of growth, viz., the spore stage. In the absence of a test sufficiently sensitive to detect fermentation by a single spore, other means must be employed. The experiments reported herein were designed to test the fermentative abilities of tetrads derived from "converting" pedigrees under conditions in which their multiplication was restricted and therefore before their chances of mutation had obscured the results.

Previous pedigrees in which irregular segregations of galactose and melibiose markers were analyzed (Lindegren and Lindegren, 1946, table 2) were derived from crosses in which culture C1A was used as one of the parents. It is a single-spore culture derived from S. *carlsbergensis* (culture 126, Dr. Mrak) and its use as a parent causes marked disturbances in segregations in the progeny. It is an *a* mating type capable of fermenting sucrose, galactose, melibiose, alpha methyl glucoside and maltose; C1A is an adenine-independent white culture and is thiamin-, inositol-, and pantothenate-independent but is pyridoxine-dependent. The asci descended from C1A analyzed by Lindegren and Lindegren were characterized for only mating type specificity and galactose and melibiose fermentations. Moreover, these asci were produced by inducing mass copulations of haploid parents and the limited number of marker genes made their truly hybrid nature a debatable question.

In the present investigation, a sufficient number of marker genes was used to establish hybridity beyond any question. The use of the adenine-dependent, pink

haplophase cultures as mates for C1A and its close descendants afforded an added advantage. The pink cultures were descendants of a white clone treated with nitrogen mustard gas by Dr. E. L. Tatum and Mr. S. E. Reaume.

EVIDENCE THAT CONVERSIONS OF FERMENTER GENOTYPES ORIGINATE IN THE HETEROZYGOTE

Materials and methods: Five different crosses involving C1A and three of its direct descendants (607, 608, and 609) were made:—C1A $\times$ 3349; 609 $\times$ 3190; 607 $\times$ 3168; C1A $\times$ 5859; and 608 $\times$ M317. The spores were isolated on natural medium with glucose as a carbon source. Only 34 four- and three-spored viable asci from a total of 87 dissected have been included in the present analyses.

After all the four (or three) spores in a tetrad had germinated to produce microcolonies ranging in population from 100,000 to 500,000 cells per colony, each entire microcolony was transplanted and streaked over a small area on a glucose agar slant. This procedure insures a thorough mixing of mutant fermenter sectors that might have arisen during growth of the microcolony. A small number of cells was then immediately scraped off the slant surface and inoculated into molten 1.75 per cent nutrient agar at 40° C. containing 2 per cent galactose as the carbon source. This molten agar was poured over a layer of solidified non-nutrient 3 per cent agar in a sterile Petri plate. A third layer of non-nutrient agar was poured over the galactose agar after the latter had solidified. This method prevents the fermenter colonies in close proximity from being confluent in growth and also minimizes contaminations. The same procedure was employed in making melibiose pour-plates. Fig. 1 describes the method diagramatically.

The residual haplophase yeast on the slant was allowed to incubate 24 hours and was then streaked over the entire slant surface to obtain luxuriant growth. This tube was retained as the stock culture. Mature inoculum from the glucose slant was subsequently tested for mating type specificity and fermentative and vitamin-synthesizing abilities. Simultaneous tests for galactose and melibiose fermentation by colonies developing on galactose and melibiose pour-plates were conducted.

The data are presented in tables I–V. The capitals *G, ME, MG, S,* and *MA* indicate phenotypes fermenting galactose, melibiose, alpha methyl glucoside, sucrose, and maltose, respectively; the corresponding small letters denote the recessive, non-fermenter alleles. The number of days elapsing before a "slow" clone ferments is indicated by subscript numerals. White cultures are indicated by W and pink ones by P. Adenine-independence is denoted by *AD* while dependence is shown by *ad*. The alleles *TH/th, PN/pn, IN/in, PY/py* indicate abilities (or inabilities) to synthesize thiamin, pantothenate, inositol and pyridoxine, respectively.

EXPERIMENTAL RESULTS

The widespread disturbances in segregations of fermenter phenotypes (shown in tables I–V) are noteworthy, since the stocks to which C1A, 607, 608 and 609 were mated had been carefully selected for regular segregations for the characters.

Cells from smear immediately transferred into galactose pour-plate, incubated and tested for galactose fermentation

Haplophase microcolonies of a single tetrad on glucose-agar droplets

Cells from smear immediately transferred into melibiose pour-plate, incubated and tested for melibiose fermentation

Inoculum from glucose slant, after luxuriant growth, is tested directly for mating type, ability to ferment sugars and synthesize vitamins
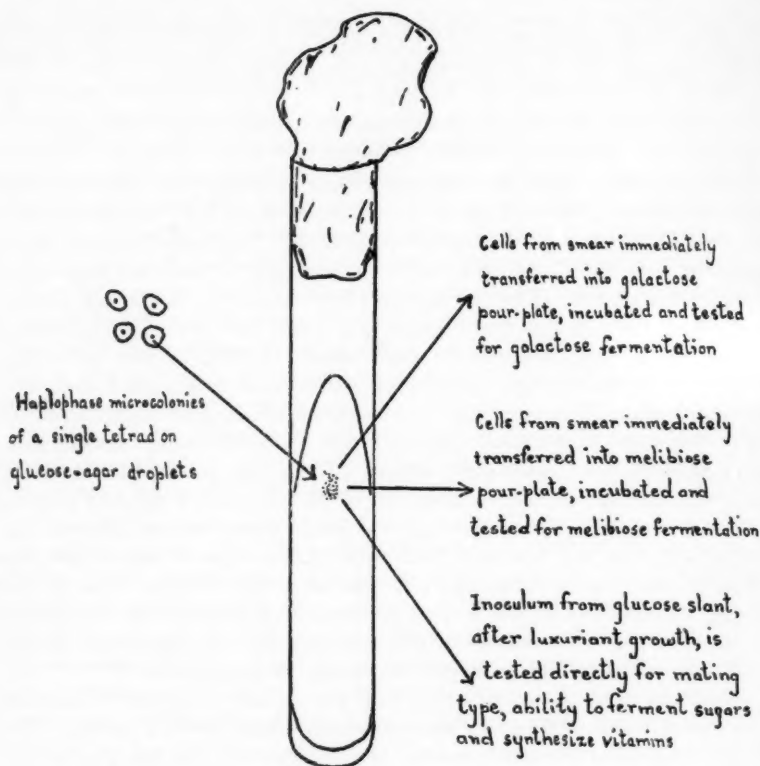
Fig. 1. Diagram showing the procedure adopted to minimize mutations in single spore clones and correlate fermentative capacities during two growth periods of a haplophase segregant.

In spite of the extensive non-Mendelian ratios, the truly hybrid nature of the asci analyzed is evident from the regular segregations of at least two marker genes in each ascus. Further support derives from the fact that cultures of C1A, 607, 608, and 609, and their mates are unable to copulate illegitimately and produce ascospores.

The possibility that a high rate of mutation of the non-fermenter recessive genes to dominance or of the fermenter gene to recessiveness would explain the irregularities in segregation was excluded by the fact that the haploid clones to which C1A, 607, 608, and 609 were mated had been derived from pedigrees in which the stability of the genotypes was pronounced. Further confirmation of the stability of the recessive parents was obtained by the procedure for detecting fermentation mutants described previously (Mundkur and Lindegren, 1949). No reversions to melibiose fermentations were detected in fifteen melibiose pour-plates

made with heavy inocula of glucose-grown, melibiose non-fermenter clones; the rates of reversion of galactose recessives were very low.

SEGREGATIONS OF GALACTOSE AND MELIBIOSE FERMENTER PHENOTYPES

It has been pointed out above that the ambiguity in deciding whether the extra-fermenters in *G G G g* and *G G G G* (or *ME ME ME me* and *ME ME ME ME*) tetrads originate from gene transformations or from mutations can be resolved by minimizing the chances of mutations in a haplophase segregant. The galactose and melibiose pour-plates made with inoculum obtained directly from the microcolonies provided data on this point. Since the mutation rates observed are usually of the order of 1×10^{-7} and the number of cells in a microcolony at the time of pouring plates does not exceed 500,000, the probability of recovering fermenter mutants may be assumed to be rather remote at this stage of growth. This assumption is strengthened, moreover, by the demonstration (cf. above) of the stability of the genotypes in the recessive parents.

The colonies in pour-plates of both galactose and melibiose agar are principally of three sizes on the fourth or fifth day after plating. These have been arbitrarily designated as large, medium, and minute colonies. The large colonies range in diameter from approximately 0.8 to 6 mm., while the medium-sized colonies are approximately 0.2 to 0.5 mm. in diameter. The minute colonies are visible as specks in the agar.

When a haploid clone is plated out, it may develop into uniformly sized colonies falling in any one of these categories, or a combination of two of these size classes; or it may show no growth at all. In tables I–V when one class alone is indicated for a segregant, it is implied that the colonies in that particular pour-plate are of uniform size. Plate 1 shows melibiose pour-plates of tetrad M532–M535, exemplifying these size classes.

The medium- and large-sized colonies are obviously fermenters and consistently corroborate the phenotype of the segregant obtained from the corresponding glucose slant. However, the minute colonies may or may not be fermenters. For instance, on plates where both minute and large colonies occur, single minute colonies inoculated with a micropipette into sugar broth achieve fermentation and confirm the characteristic of the clone from the corresponding slant. In other cases, however, minute colonies occurring uniformly in a plate were generally non-fermenters.

Evidence that the differences in colony sizes in a fermenter clone result not from differences in fermentative ability but really from differing growth rates was obtained from the following experiment: A suspension of a single minute fermenter colony (clone M533) from a galactose plate was plated out in galactose agar and was found to yield only minute colonies. A galactose pour-plate of a suspension of a single large fermenter colony of the same clone produced both large and minute colonies. Therefore, the minute colonies are slower-growing clones descended from the large-colonied clones. This explains the occurrence of

TABLE I

TETRAD ANALYSIS OF CONVERTER BY STANDARD HYBRID ASCI, *C1A* BEING THE CONVERTER

(*C1A* α *G ME MG MA AD*(W) *TH PN IN py* × 3349 a *g me mg ma ad*(P) *TH pn in py*)

Tetrad phenotypes								Size of colonies in pour-plates		Fermentation by inocula from pour-plates	
Inocula derived from glucose slants								Gal. plates	Mel. plates	Gal. plates to gal. broth	Mel. plates to mel. broth
M528 a	*G*	*ME*	*MG*	*MA*	*AD* (W)	*pn*	*in*	med.	lge.	+	+
M529 α	*G*	*ME*	*MG*	*MA*	*AD* (W)	*pn*	*IN*	med.	min.	+	+
M530 α	*G*	*ME*	*MG*	*MA*	*AD* (W)	*PN*	*IN*	med.	min.	+	+
M531 a	*G*	*ME*	*MG*	*MA*	*AD* (W)	*PN*	*in*	med.	lge.	+	+
M532 α	*G*	*ME*	*MG*	*MA*	*ad* (W)	*pn*	*in*	lge.	lge.	+	+
M533 α	*G*	*ME*	*MG*	*ma*	*ad* (W)	*pn*	*in*	min. & lge.	med.	+	+
M534 a	*g*	*ME*	*MG*	*MA*	*AD* (W)	*PN*	*IN*	min.	lge.	−	+
M535 a	*g*	*me*	*MG*	*MA*	*AD* (W)	*PN*	*IN*	min.	min.	−	−
M536 α	*g*	*ME*	*mg*	*ma*	*ad* (P)	*pn*	*in*	min.	med.	−	+
M537 a	*G*	*ME*	*mg*	*MA*	*AD* (W)	*pn*	*in*	min.	med.	+	+
M538 α	*g*	*me*	*mg*	*MA*	*ad* (P)	*PN*	*IN*	min.	min.	−	−
M539 a	*G*	*me*	*MG*	*ma*	*AD* (W)	*PN*	*IN*	min.	min.	+	−
M540 ?	*G*	*ME*	*MG*	*MA*	*AD* (W)	*pn*	*IN*	med.	min.	+	+
M541 ?	*G*	*ME*	*MG*	*MA*	*AD* (W)	*pn*	*IN*	med.	min.	+	+
M542 ?	*G*	*ME*	*MG*	*MA*	*AD* (W)	*pn*	*in*	med.	min.	+	+
M543 ?	*G*	*me*$_{12}$	*MG*	*MA*	*ad* (W)	*PN*	*in*	med. & min.	min.	+	+$_{17}$
M544 a	*G*	*me*	*MG*	*MA*	*ad* (W)	*PN*	*IN*	lge.	no growth	+	−
M545 a	*G*	*ME*	*MG*	*MA*	*AD* (W)	*pn*	*IN*	med.	med.	+	+
M546 α	*G*	*me*	*MG*	*MA*	*ad* (W)	*pn*	*in*	med.	no growth	+	+
M547 a	*G*	*ME*	*MG*	*MA*	*AD* (W)	*PN*	*in*	med. & lge.	med.	+	+
M548 α	*G*	*ME*	*MG*	*ma*	*ad* (P)	*PN*	*in*	med.	med.	+	+
M549 α	*G*	*me*	*MG*	*MA*	*ad* (P)	*PN*	*IN*	lge.	min.	+	+
M550 a	*g*	*ME*	*mg*	*ma*	*AD* (W)	*pn*	*IN*	min.	med.	−	+
M551 a	*g*	*me*	*mg*$_2$	*MA*	*AD* (W)	*pn*	*in*	min.	min.		
M552 α	*G*	*ME*	*mg*	*MA*	*AD* (W)	*PN*	*IN*	med. & lge.	med. & lge.	+	+
M553 a	*G*	*ME*	*MG*	*MA*	*AD* (W)	*pn*	*IN*	min. & lge.	med.	+	+
M554 α	*R₃*	*me*$_4$	*MG*	*MA*	*ad* (W)	*pn*	*in*	min.	no growth	+?	−
M555 a	*G*	*me*$_4$	*MG*	*ma*	*AD* (W)	*PN*	*IN*	min.	no growth	+	−
M556 α	*g*	*ME*	*mg*$_5$	*ma*	*ad* (P)	*pn*	*IN*	min.	med.	−	+
M557 α	*g*	*ME*	*mg*	*MA*	*ad* (P)	*PN*	*IN*	min.	min.	−	+
M558 a	*G*	*me*	*mg*	*ma*	*AD* (W)	*pn*	*IN*	med.	min.	+	−
M560 α	*G*	*ME*	*mg*	*MA*	*AD* (W)	*PN*	*IN*	med.	med..	+	+
M561 a	*g*	*me*	*MG*	*ma*$_5$	*ad* (W)	*pn*	*in*	min.	no growth	−	−
M562 a	*G*	*ME*	*MG*	*MA*	*ad* (W)	*PN*	*in*	lge.	lge.	+	+
M563 α	*G*	*ME*	*MG*	*MA*	*AD* (W)	*pn*	*IN*	lge.	lge.	+	+
M564 a	*G*	*ME*	*MG*	*MA*	*AD* (W)	*PN*	*IN*	med.	min. & lge.	+	+
M565 α	*G*	*me*	*MG*	*MA*	*AD* (W)	*PN*	*in*	med.	no growth	+	−
M566 α	*G*	*ME*	*MG*	*MA*	*AD* (W)	*PN*	*in*	min. & med.	med.	+	+
M567 α	*G*	*ME*	*MG*	*MA*	*AD* (W)	*PN*	*IN*	med.	lge.	+	+
M568 α	*G*	*ME*	*MG*	*MA*	*ad* (P)	*PN*	*IN*	med.	med.	+	+
M569 a	*G*	*ME*	*MG*	*ma*	*AD* (W)	*pn*	*in*	med.	med.	+	+

fermenter colonies of two size classes in the same plate. However, the fact that when only minute colonies occur on a plate, they are generally non-fermenters indicates that the genotype is intrinsic in the spore from which the clone descended.

The uniformity in size of pour-plate colonies in a large number of tetrads is, in itself, strong evidence that mutations with regard to fermentative ability did not occur with sufficiently high frequency to be detectable in the microcolony.

In determining the fermentative abilities of the minute colonies, large numbers of them were inoculated into the same broth tube to establish their phenotype with greater certainty. This is especially important when the corresponding glucose slant clone is a non-fermenter. The use of a large number of minute colonies insures that corroboration of the non-fermenter phenotype from glucose was not coincidental. On the other hand, the extra-fermenters in a tetrad would have been diagnosed as such if only a single mutation (g to G; me to ME) occurred on a slant; or, if there were a single fermenter colony amidst the more numerous non-fermenter colonies and this exceptional one were inoculated into sugar broth together with its sister, non-fermenter colonies.

To test for variation among the individual colonies on a plate in the tetrads with extra-fermenters, the following experiment was performed: Two representative tetrads having extra-fermenters were selected (M532–M535; M544–M547) and the clones known to be galactose- and melibiose-fermenters were plated out in glucose nutrient agar directly from the original glucose slant. Ten individual colonies picked at random from each plate were inoculated each into a separate galactose (or melibiose) Durham fermentation tube. All tubes contained gas within 24 hours. This experiment indicates that individual colony variation as regards galactose and melibiose fermentations did not occur in the pour-plate. It also confirms the fact that after an originally recessive, non-fermenter clone has acquired fermentative ability (and thus become the extra-fermenter in the tetrad) this new capacity is not affected by an intervening period of growth on glucose.

Tetrads M488–M491 and M500–M503 (table II) exemplify a situation one would expect as a corollary to the cases of the extra-fermenter tetrads discussed above. The haplophase parents C1A and 607 involved in the crosses analyzed in tables I, III and V are members of the "converting pedigree" and bear the dominant G and ME alleles. The occurrence of extra-fermenters in these crosses has been explained above as being due to a transfer of gene material from the G to the g (or ME to the me) allele. However, 609 (a parent of M488-M503, table II), which is also a member of the "converting pedigree," bore the recessive me allele and was mated to a ME clone (3190) derived from a regularly segregating (ME/me) pedigree. Tetrads M488–M491 and M500–M503 obtained from this cross include more than the two expected me clones, indicating that the recessive allele in the converter, i.e., in 609, can degrade the ME allele of its mate which descended from a pedigree in which the ME/me alleles segregate regularly. At the same time an excess of G phenotypes are produced in the same asci.

The occurrence of three non-fermenter segregants in each tetrad is explained on the following basis: During meiosis the *me* gene from the converter parent acquires some essential gene component from the homologous dominant allele of its mate (3190). This acquisition is not sufficient to elevate the *me* allele to functional activity, but the degradation of the *ME* gene is sufficiently severe to negate its normal function. The single fermenter segregant in each tetrad was presumably not affected or, at least, was apparently not degraded below the critical threshold.

TABLE II

TETRAD ANALYSIS OF CONVERTER BY STANDARD HYBRID ASCI, 609 BEING THE CONVERTER

(609 α *G me MA AD*(W) *TH IN py pn* × 3190 a *g ME ma ad*(P) *th in PY PN*)

Tetrad phenotypes									Size of colonies in pour-plates		Fermentation by inocula from pour-plates	
Inocula derived from glucose slants									Gal. plates	Mel. plates	Gal plates to gal. broth	Mel. plates to mel. broth
M488	α	*G*	*me*	*MA*	*AD*	(W)	*TH*	*in*	med.	no growth	+	−
M489	α	*G*	*me*	*MA*	*AD*	(W)	*TH*	*IN*	med.	no growth	+	−
M490	a	*G*	*me*	*MA*	*AD*	(W)	*TH*	*IN*	med.	no growth	+	−
M491	a	*G*	*ME*	*ma*	*AD*	(W)	*th*	*in*	med.	med.	+	+
M492	α	*G*	*ME*	*MA*	*AD*	(W)	*TH*	*in*	med. & lge.	med.	+	+
M493	a	*G*	*me*	*MA*	*ad*	(W)	*TH*	*IN*	med. & lge.	min.	+	−
M494	a	*G*	*me*	*ma*	*ad*	(W)	*th*	*in*	med. & lge.	min.	+	−
M496	a	*G*	*ME*	*MA*	*AD*	(W)	*TH*	*IN*	med.	lge.	+	+
M497	α	*g*	*me*	*MA*	*ad*	(W)	*th*	*in*	no growth	min.	−	−
M498	α	*g*	*me*	*MA*	*ad*	(W)	*th*	*in*	no growth	min.	−	−
M500	α	*G*	*me*	*MA*	*ad*	(P)	*TH*	*IN*	min. & med.	min.	+	−
M501	a	*G*	*me*	*MA*	*ad*	(W)	*th*	*in*	med.	no growth	+	−
M502	α	*G*	*ME*	*MA*	*ad*	(P)	*TH*	*in*	med.	med.	+	+
M503	a	*g*	*me*	*MA*	*ad*	(W)	*th*	*in*	min.	min.	−	−

TABLE III

TETRAD ANALYSIS OF CONVERTER BY STANDARD HYBRID ASCI, 607 BEING THE CONVERTER

(607 a *G ME ma AD*(W) × 3168 α *g me MA ad*(P))

Tetrad phenotypes							Size of colonies in pour-plates		Fermentation by inocula from pour-plates	
Inocula derived from glucose slants							Gal. plates	Mel. plates	Gal. plates to gal. broth	Mel. plates to mel. broth
M508	?	*G*	*ME*	*ma*	*ad*	(W)	med.	med.	+	+
M509	?	*g*	*ME*	*ma*	*ad*	(W)	no growth	med.	−	+
M510	?	*G*	*ME*	*MA*	*AD*	(W)	lge.	med.	+	+
M511	?	*G*	*ME*	*MA*	*AD*	(W)	lge.	med.	+	+
M512	?	*G*	*ME*	*ma*	*AD*	(W)	lge.	lge.	+	+
M513	?	*G*	*ME*	*ma*	*ad*	(W)	lge.	lge.	+	+
M514	?	*g*	*ME*	*MA*	*AD*	(W)	min.	med.	−	+

TABLE IV

TETRAD ANALYSIS OF CONVERTER BY STANDARD HYBRID ASCI, 608 BEING THE CONVERTER

(608 a g me mg S MA AD(W) TH IN PN py × M317 α G ME MG S ma ad(P) th in pn py)

Tetrad phenotypes (Inocula derived from glucose slants)	Size of colonies in pour-plates — Gal. plates	Size of colonies in pour-plates — Mel. plates	Fermentation — Gal. plates to gal. broth	Fermentation — Mel. plates to mel. broth
M591 α G me MG S MA AD (W) TH IN pn py	med.	min.	+	—
M592 a G me MG S MA ad (W) th in pn py	med.	no growth	+	—
M593 a G me mg S MA ad (W) th in pn py	med.	no growth	+	—
M594 α G me mg S MA AD (W) TH IN pn py	no growth	min.	—	—
M595 a G me mg_3 S MA AD (W) TH IN pn py	min. & med.	min.	+	—
M596 a G me MG S MA AD (W) TH IN PN py	med.	min.	+	—
M597 α g me mg S MA ad (W) th in pn py	min.	no growth	—	—
M598 α G me mg S MA ad (W) th in pn py	min. & med.	no growth	+	—
M599 a g_6 me MG S MA ad (W) th in pn py	med.	min.	+[6]	—
M600 a g_7 me MG S MA AD (W) TH IN pn py	med.	min.	+[6]	—
M601 α G me mg S MA ad (W) th in PN py	med.	no growth	+	—
M602 α G me mg S MA ad (W) th in pn py	lge.	no growth	+	—
M603 α g_6 me mg S ma AD (W) TH IN PN py	med.	min.	+[6]	—
M604 a G me mg_6 S MA ad (W) th in pn py	lge.	no growth	+	—
M605 α g me MG S ma ad (W) th in pn py	min.	no growth	—	—
M606 a g_4 me mg_4 S MA AD (W) TH IN PN py	med.	min.	+	—
M607 a G me MG S MA AD (W) TH in pn py	med.	min.	+	—
M608 a G me mg S MA AD (W) TH IN pn py	med.	min.	+	—
M609 α g_7 me mg S MA ad (W) th in pn py	med.	no growth	+[6]	—
M610 α g me MG S MA ad (W) th in pn py	min.	no growth	—	—
M611 α G me mg S MA ad (W) th in pn py	lge.	no growth	+	—
M612 a g_6 me mg_6 S ma ad (W) th in pn py	med.	no growth	—	—
M613 a G me mg_4 S MA AD (W) TH IN pn py	lge.	min.	+	—
M614 α G me MG S MA AD (W) TH IN pn py	med.	min.	+	—
M615 a G me MG S MA AD (W) TH IN PN py	lge.	min.	+	—
M616 α G me mg S MA ad (W) th in pn py	med.	min.	+	—
M617 a g_7 me MG S ma ad (W) th in pn py	med.	min.	+[6]	—
M618 α G me mg S MA ad (W) th in pn py	lge.	min.	+	—
M619 a g_6 me MG S MA ad (W) th in pn py	med.	min.	+	—
M620 α G me MG S MA AD (W) TH IN pn py	lge.	min.	+	—
M621 a g_6 me mg S MA ad (W) th in pn py	med.	no growth	+[9]	—
M622 α g me mg S ma AD (W) TH IN PN py	min.	no growth	—	—
M623 α g me MG S MA AD (W) TH IN pn py	min.	min.		—
M624 α G me mg S MA ad (W) th in pn py	lge.	no growth	+	—
M625 a G me mg S MA AD (W) th IN pn py	lge.	no growth	+	—
M627 a g me MG S ma_6 ad (W) th in pn py	no growth	no growth	—	—
M628 a G me mg S MA ad (W) th in pn py	lge.	min.	+	—
M629 α g me mg S MA AD (W) th in pn py	min.	min.	—	—
M630 α g me MG S MA AD (W) TH IN pn py	no growth	no growth	—	—
M631 a G me MG S MA ad (W) th in pn py	lge.	no growth	+	—
M632 α G me mg S MA ad (W) th in pn py	lge.	min.	+	—
M633 α g_7 me mg S MA AD (W) TH IN PN py	med.	min.	+[7]	—

TABLE V

TETRAD ANALYSIS OF A CONVERTER BY STANDARD HYBRID ASCI, *C1A* BEING THE CONVERTER

(*C1A* α *G ME S MG MA AD TH IN PN py* × 5859 a *g ME s MG MA AD TH IN PN PY*)

Tetrad phenotypes		Fermentation by inocula from pour-plates
Inocula derived from glucose slants	Size of colonies in gal. pour-plates	Gal. plates to gal. broth
M464 α *G ME s MA MG TH py*	large	+
M465 α *G ME S MA MG TH py*	large	+
M466 a *G ME S MA MG TH PY*	medium	+
M467 a *G ME S MA MG TH PY*	medium	+
M468 α *G ME s MA MG TH py*	medium	+
M469 a *G ME S MA MG TH PY*	medium	+
M470 α *g ME S MA MG TH py*	minute	−
M471 a *g ME S MA MG TH PY*	minute	−
M472 a *G ME s MA MG TH PY*	large	+
M473 α *G ME S MA MG TH PY*	large	+
M474 α *G ME S MA MG TH py*	large	+
M475 a *G ME S MA MG TH py*	large	+
M476 a *G ME S MA MG TH PY*	medium & large	+
M477 α *G ME S MA MG TH PY*	medium	+
M478 a *G ME S MA MG TH py*	medium	+
M479 α *G ME S MA MG TH py*	medium	+
M480 a *G ME S MA MG TH PY*	large	+
M481 α *g ME S MA MG TH PY*	no growth	−
M482 α *G ME S MA MG TH PY*	large	+
M484 α *G ME s MA MG TH py*	medium	+
M485 α *G ME S MA MG TH PY*	medium	+
M486 a *G ME S MA MG TH py*	medium	+

Even more striking instances of gene degradations are evident in clones M591 to M633. In contrast to the mating 609 × 3190, which involved the melibiose gene as the only recessive converter among the sugar markers used, mating 608 × M317 (table IV) involved four heterozygous sugar markers with the converter parent carrying the recessives *g*, *me*, and *mg*. The total absence of progeny capable of producing gas from melibiose in the Durham tubes in all the tetrads derived from this cross is notable, and is perhaps indicative of a marked instability of the dominant gene controlling the fermentation of melibiose. It is also interesting that, with one exception, each tetrad comprises two clones yielding minute colonies in melibiose pour-plates and two showing no growth. Three tetrads from the same cross also include a deficiency of *G* clones, while three other tetrads include an excess of *G* segregants. The absence of any 4:0 *G:g* tetrads is significant. In addition, 10 "slow"-fermenters of galactose were obtained.

The converter 608 carried the dominant *MA* allele, and tetrads obtained by mating this clone to M317 (which carried the recessive, *ma*) generally comprise an excess of maltose fermenters (usually 4:0). Similar cases of 4:0 segregations when

the converter parent carried dominant alleles for fermentative ability can be seen in other crosses.

The significant point is that the phenomenon is non-specific. That is, the presence of the recessive gene in a converter parent need not always result in tetrads with an excess of recessive progeny, for it is conceivable that the dominant allele may not necessarily be completely degraded. The recovery of 4:0, fermenter: non-fermenter progeny from crosses of dominant converters by recessive, standard clones suggests that the dominant gene in the converting parent is not degraded so severely as in cases involving crosses of dominant, standard clones by recessive converters. Converter haploids may thus differ from standard haploids in possessing a more pronounced lability of the genotype, although the detection of truly non-Mendelian segregations in crosses involving two standard clones is by no means rare.

The data presented above eliminate the possibility that non-Mendelian tetrads arise from mutations during the growth of originally Mendelian tetrads on glucose. The exclusion of mutations as a possible cause of irregular ratios leaves open polysomy and polyploidy as possible mechanisms. Rather, the data suggest that irregular segregations of the abilities to ferment galactose and melibiose may originate in the heterozygous condition owing to gene conversions.

NON-MENDELIAN SEGREGATIONS AT OTHER LOCI

The view that non-Mendelian ratios arise from gene conversions in the heterozygote rather than from chance mutations has been confirmed above only with respect to galactose and melibiose fermentations. No attempt was made to verify irregular ratios of other sugar markers (sucrose, alpha methyl glucoside, and maltose) using pour-plates of tetrads as checks. The widespread irregular segregations of these markers suggests, however, that conversion of alleles was operative here also.

A few "slow"-fermenter clones are listed in tables I and IV. "Slow" fermentation of galactose was analyzed in a previous report (Mundkur and Lindegren, 1949) where it was shown to result from selection in galactose broth of G mutants descended from originally g segregants. In the present analyses, no attempt was made to determine whether the "slow" fermenters are similar to those previously analyzed or result from a delayed phenotypic expression of gene conversions because of the obvious difficulties involved in making such a distinction.

Segregations of vitamin-synthesizing abilities were also irregular, exceptional tetrads occurring with higher frequency than are encountered in standard pedigrees. Table VI summarizes the frequency of irregular tetrads.

TABLE VI

NON-MENDELIAN INHERITANCE OF VITAMIN-SYNTHESIZING ABILITIES IN TETRADS
SHOWN IN TABLES I TO V. ONLY 4-SPORED AND OBVIOUSLY NON-MENDELIAN
3-SPORED ASCI ARE INCLUDED.

Vitamin	Number of heterozygous asci marked for the vitamin	Frequency of non-Mendelian asci
Thiamin	11	4
Inositol	20	7
Pantothenate	19	11
Pyridoxine	5	2

In addition to the disturbances in segregations of sugar markers, the irregularities in inheritance of adenine-synthesizing ability are very pronounced. It has been shown (Lindegren and Lindegren, 1947) that pink haploids result from the inability to synthesize adenine and that white clones are generally adenine-independent. Occasional tetrads with excess of white progeny out of a pink $\times$ white mating have been interpreted as being due to depletions of pinks. The pink color was restored to activity following outcrosses.

The irregular ratios for the $AD(W)/ad(P)$ alleles in the present analyses are presumably conditioned by the same mechanism. Several tetrads shown in the tables comprised four white progeny out of a pink $\times$ white cross but in some, two clones are $ad(W)$ and two are $AD(W)$. This fact further confirms the hybridity of the asci analyzed.

Disturbances in mating reactions are also noteworthy. In testing for mating type specificity, a heavy inoculum of each of the four segregants from a tetrad is held in glucose broth together with a standard a clone known to copulate vigorously with other haploids. A positive mating reaction identifies its mate as an "a" mating type; in the absence of copulations, the mate is diagnosed as a clone of like mating type, i.e., as an α mating type. Copulations are generally effected within a few hours. In the present analyses, mating type specificity segregated 2a/2α. Occasional disturbances in mating reactions were, however, encountered. For instance, tetrad M528–M531 (W W W W) was mated to the standard a clone but no copulations were observed until the fifth day; tetrads M536–M539, and M548–M551 (2 P:2 W) had the normal mating strength and copulated vigorously within twelve hours. Other tetrads (table I), none of whose haplophases copulated with the standard a clones even on the fifth day, were subsequently mated with a standard a clone, and two of the haplophases from each of these tetrads copulated vigorously. Still others, M540–M543 (table I) and M508–M514 (table III) mated with neither the α nor the a standard clones. Similar instances of W W W W tetrads failing altogether to copulate are cited in Lindegren (1949) and Mundkur and Lindegren (1949).

The fact that mating strength is normal in 2 P:2 W asci but is impaired or absent in some W W W W asci (obtained from P $\times$ W crosses) suggests that the phenomenon is in some way associated with disturbances at the AD/ad loci. Further investigation of mating type reactions was not undertaken.

DISCUSSION

Winkler's (1930, 1932) proposal of the Konversions-Theorie was an attempt to explain deviations from the expectations of tetrad analysis which could not be satisfactorily explained by the theory of crossing-over. Winkler's 1932 paper is the most ambitious attempt at refuting arguments levelled against his theory by Stern (1930, 1931, 1932), who insisted that the deviations cited by Winkler did not invalidate the theory of crossing-over.

Winkler's Konversions-Theorie postulates a physiological transition of the gene from one physiological condition to another during the maturation divisions. According to him, "monogenic" conversions involve the transformation of the recessive gene alone into a dominant one; or a transformation of the dominant alone into the recessive condition. When, however, the recessive gene acquired dominance while, simultaneously, the dominant allele transformed into recessiveness, the conversion was "digenic." The experiments reported in the present paper have justified Winkler's insistence on the necessity of performing tetrad analyses as a means of determining whether irregular segregations arise from conversions or exclusively from cross-overs or other chromosomal aberrations. However, owing to the precision with which the crossing-over theory can predict map distances, his view that conversions can explain all cases interpreted as cross-overs seems far fetched. When adequate tetrad analyses are available it is possible to distinguish those cases involving conversions from those involving crossing-over. Monogenic conversions can be detected unambiguously when segregations in a monohybrid tetrad show unequal frequencies of the dominant and recessive genes. It is simpler to assume that what Winkler termed digenic conversions are actually cross-overs since the results of this phenomenon lead so clearly to the prediction to map distances.

Zickler (1934) made exhaustive genetical investigations on the heterothallic ascomycete *Bombardia lunata*. Tetrad analyses of pedigrees heterozygous for *rubiginosa/viridis* revealed high frequencies of non-Mendelian ratios among several thousands of asci. Such exceptional asci contained spore tetrads exhibiting 6:2 and 8:0 *rubiginosa/viridis* segregations. These markers involved spore color and, though morphological, the characters could be distinguished from each other with great precision, in contrast to many morphological markers whose diagnosis is often ambiguous. To explain deviations in segregations from the Mendelian expectations in *B. lunata*, Zickler invoked the Konversions-Theorie and held that crossing-over cannot explain the *monogenic* conversions encountered.

Wülker (1935) analyzed numerous crosses in *Neurospora sitophila,* and observed significant divergences from Mendelian expectations. He described perithecia in which the asci exhibited either a 4:4, 0:8, or 2:6 segregation, exclusively; other

perithecia—the so-called "Mischperithecien"—in which all these three ascus types occurred were also found. The high frequencies of irregular segregations he discovered are evident from his data for the mixed perithecia:

4:4 segregations = 30 asci (19.9 per cent)

2:6 segregations = 92 asci (60 per cent)

0:8 segregations = 29 asci (19.2 per cent)

Perithecia showing only one ascus type:

4:4 segregations = 0 asci

0:8 segregations = 89 asci

However, in spite of these discrepancies, Wülker could not decide in favor of any one of the three explanations for divergent asci he suggested as possible: the labile nature of the gene, conversions, and the influences of environmental factors. This, indeed, is not surprising for he investigated only a single pair of markers L/l (the formation of *Luftmyzel* or its absence) in the non-Mendelian pedigrees.

In addition to the non-Mendelian segregations discovered in *Bombardia* and *Neurospora,* numerous instances of exceptions to Mendelian ratios are known in the fungi. Such irregularities occur in *Coprinus fimetarius* (Brunswik, 1926); *Ustilago levis* (Dickinson, 1928); *Aleurodiscus* (Kniep, 1928); *Phycomyces blakesleeanus* (Burgeff, 1928); *Ustilago zeae* (Hanna, 1929; Christensen, 1931); *Sphacelotheca* (Rodenhiser, 1932); *Sphaerocarpus* (Allen, 1930); *Hypomyces Ipomoeae* (Dimock, 1939). However, in none of these fungi are chromosome maps available; and these are required to distinguish actual non-Mendelian segregations from aberrant ratios arising from segregations of polymeric hybrids or from segregations of hybrids carrying duplications.

The unique advantages of tetrad analysis are obvious, and it is not surprising that irregular segregations are encountered more frequently in the fungi, where tetrad analysis is feasible, than in higher organisms, where it is not. When higher organisms are used as genetic material, the conclusive detection of irregular segregations is either impossible or the chances of detecting true conversions are, at best, greatly reduced. This limitation derives from the fact that since tetrad analysis is not possible in these organisms regular gametic segregations have been *assumed* to occur. During animal oogenesis, for instance, a regular 2:2 segregation of genes among the nucleus in the egg cell and the three polar bodies is only *inferred* provided an approximately 1:1 ratio is obtained when a heterozygous female is mated to a recessive male. Similar inferences are also made with regard to microsporogenesis and megasporogenesis in higher plants. These inferences regarding the ratios of segregations among the gametes can be based only on the recombinations of the markers in the F_1 generation since the products of meiosis are not directly accessible for characterization. Apparent instances of irregular segregations can be explained on the basis of ploidy or crossing-over if they can be verified by cytological methods. However, significant deviations from 1:1 segregations among the progeny of a hybrid higher plant or animal are *assumed* to be

due to preferential survival of sperm or eggs carrying the dominant allele, or to some chromosomal aberration.

Tetrad analyses of all the nuclei originating from the same mother cell have, in yeast, yielded vital information inconsistent with the assumptions and inferences involved in the genetical analyses of higher plants and animals. A knowledge of linkage groups in *Saccharomyces* has been of especial usefulness.

The necessity for tetrad analysis in evaluating the status of non-Mendelian inheritance lies in the accessibility to *all* the haploid products of meiosis for a *direct* characterization. Unlike higher organisms where the F_1 generation is analyzed, tetrad analysis in the fungi is not obscured by dominance effects or by the ambiguities concerning survival of the products of reduction or of competitions between them resulting in selective fertilization. Moreover, when enough markers are employed, recourse to tetrad analysis makes genetical characterizations of large numbers of progeny a relatively unimportant matter. When biochemical criteria are used, as in the present investigation, tetrad analysis acquires an added significance. Segregations of abilities or inabilities to ferment various sugars, synthesize vitamins and other cell components are gene-controlled and can therefore be diagnosed without ambiguity. Where the recessive markers used are especially "good" (examples: *g, me, ma, mg, ad, th, in, pn, py*) the segregations are exceptionally clear-cut.

TABLE VII

EXPECTATIONS OF DOMINANT AND RECESSIVE PHENOTYPES WHEN DOUBLE DOMINANT OR DOUBLE RECESSIVE DISOMICS (*PP; pp*) ARE CROSSED WITH NORMAL, HAPLOID CLONES OF OPPOSITE PHENOTYPE

Mating	Type of ascus				Ratio of phenotypes (dominants : recessives) Pp genotype = P phenotype	Frequency
	(a) PP	PP	p	p	2 : 2	1
	(b) PP	P	pP	p	3 : 1	
PP × p	(c) PP	P	p	pP	3 : 1	
	(d) P	PP	pP	p	3 : 1	4
	(e) P	PP	p	pP	3 : 1	
	(f) P	P	pP	pP	4 : 0	7
	(a) Pp	Pp	p	p	2 : 2	1
	(b) Pp	P	pp	p	2 : 2	1
pp × P	(c) Pp	P	p	pp	2 : 2	1
	(d) P	Pp	pp	p	2 : 2	1
	(e) P	Pp	p	pp	2 : 2	1
	(f) P	P	pp	pp	2 : 2	1

Among the objections raised against a gene-component transfer mechanism as an explanation for non-Mendelian inheritance, polysomy and polyploidy (Lederberg, 1948) are noteworthy. Such mechanisms, if they were operative in producing irregular ratios in *Saccharomyces*, would yield the phenotypes shown in tables VII and VIII. If we designate a dominant phenotype by P, and its alternative, recessive manifestation by p, tetrad analysis of the crosses $PP \times p$ (where PP is the disomic[1] double dominant parent) and $pp \times P$ (where pp is the disomic parent) should yield the tetrad types designated in table VII.

On the other hand, if a Pp disomic haploid originating from a heterozygous (P/p) diploid were crossed to a standard haploid clone of opposite phenotype the following tetrad types should result:

TABLE VIII

EXPECTATIONS OF DOMINANT AND RECESSIVE PHENOTYPES WHEN A Pp DISOMIC
IS CROSSED WITH A NORMAL HAPLOID CLONE OF CONTRASTING PHENOTYPE

Mating	Type of ascus				Ratio of phenotypes (dominants : recessives) pP genotype $=$ P phenotype	Frequency
	(a) pP	pP	p	p	2 : 2	1
	(b) pP	p	pP	p	2 : 2	1
$Pp \times p$	(c) pP	p	p	pP	2 : 2	1
	(d) p	pP	pP	p	2 : 2	1
	(e) p	pP	p	pP	2 : 2	1
	(f) p	p	pP	pP	2 : 2	1

A comparison of the frequencies of ascus types expected on the basis of polysomy shown in tables VII and VIII with the frequencies actually encountered in the five crosses described (tables I–V) shows obvious discrepancies. The possibility of a pp disomic effecting the irregularities is precluded by the occurrence of frequent deviations in segregation ratios in heterozygous crosses where the converter parent carried the recessive phenotype, although the only ratio expected (if a pp disomic parent were involved) is 2:2. The most striking divergences are seen in table IV where a 0:4 melibiose fermenter:non-fermenter ratio is the only one encountered; at no locus is there the required consistent 2:2 segregation in crosses where the converter carried the recessive phenotype. The possibility of a Pp disomic is also negated for the same reason since a 2:2 segregation would invariably be expected if such a disomic were involved in a cross with a normal haploid of contrasting phenotype. On the other hand, there is a significant deviation from the ratios expected if a PP parent were involved.

---

[1] The term "trisomic" describes diploid organisms having an extra chromosome. Since this term was coined particularly for normally *diploid* organisms, the term "disomic" may be used to describe a *haploid* individual bearing an extra chromosome.

TABLE IX

DISTRIBUTION OF TETRADS PRODUCED IN RECESSIVE CONVERTER × STANDARD
DOMINANT CROSSES

(Only hybrid asci heterozygous for sugar markers that were recessive in the converter parents
(tables II and IV) are included. The occurrence of unpredicted tetrad classes makes statistical
analysis irrelevant and excludes the possibility that polysomy in the haploid parents is involved.)

Ratio of fermenter:non-fermenter phenotypes	Observed frequencies			Per cent of expected frequencies
	Gal.	Mel.	α Methyl gluc.	
2:2	2	0	6	100
0:4	0	9	0	0
1:3	3	2	3	0
3:1	4	0	0	0

TABLE X

SUMMARIZED DISTRIBUTION OF TETRADS PRODUCED IN DOMINANT
CONVERTER × RECESSIVE STANDARD CROSSES

(Only those hybrids heterozygous for sugar markers (tables I to V) are included. Significant
deviations from expected ratios for galactose and melibiose markers exclude polysomy in the
dominant converter parents.)

Ratio of fermenter:non-fermenter phenotypes	Observed frequencies				Per cent of expected frequencies
	Gal.	Mel.	Malt.	α Methyl gluc.	
2:2	4	4	3	1	8.33
3:1	4	3	8	2	33.33
4:0	7	2	8	4	58.33
1:3	0	0	0	1	0
χ^2 =	9.8	15.5	2.51		
P value =	<.01	<.001	<.30		

Polyploidy is only an extension of polysomy in that every linkage group is
represented more than once in an ascospore, while in disomy only one linkage
group is represented twice in an ascospore. Some markers in the present analyses
belong in different linkage groups (for example, mating type specificity and abili-
ties to synthesize pantothenate and ferment galactose are determined by genes
located in separate chromosomes). However, the fact that in the same ascus some
markers segregate in a precisely Mendelian manner while others segregate irregularly
is *a priori* evidence for the exclusion of polyploidy as the mechanism yielding ir-
regular ratios. Lindegren (1949a) has shown that the concept of modifying genes
is inadequate to explain irregular segregations in yeasts. In the present analyses,
polymeric genes affecting melibiose fermentative ability are excluded by the oc-
currence of non-fermenter progeny among the offspring of 608, a non-fermenter
converter.

The transformed (converted) recessive haplophase clones maintain the transformed type through successive sub-culture generations, within the limits imposed by a normal mutation rate; since back mutations of transformed recessives (e. g., *me* to *ME*) do not occur in excess of expectation among the segregants recovered from a hybrid, the transformation of *ME* to *me* is not of the type already described as depletion mutation.

The high frequencies of non-Mendelian segregations discovered in the present work derive from the use of parent stocks especially conducive to evoking irregular ratios; exceptional ratios that can be interpreted only on a basis of gene conversions are, however, by no means rare even in some so-called regularly segregating pedigrees. The complete loss of ability to ferment melibiose among the offspring of a culture capable of vigorous fermentation of the sugar—a phenomenon not recorded previously—is difficult to explain on the basis of the Plasmagene Theory, and questions a long-held genetical tenet: the integrity of the gene as a Mendelian unit uncontaminable in the heterozygote.

SUMMARY

Tetrad analyses of five different crosses of *Saccharomyces* haploids with the use of biochemical markers revealed high frequencies of irregular segregation ratios. These irregularities derived from the use of certain haplophase parent stocks which, when crossed to standard haplophase clones, produced marked disturbances in segregations in the progeny. Clones effecting such disturbances have been designated as "converters."

These findings are contrary to the regular 1:1 gametic segregations expected by conventional Mendelian genetics.

In heterozygous crosses, when converter parents carrying dominant, fermenter phenotypes were mated to clones obtained from standard pedigrees, the progeny comprised an excess of fermenter segregants. Converter parents carrying the recessive, non-fermenter phenotypes, when crossed with standard clones of contrasting phenotype, yielded tetrads frequently comprising an excess of non-fermenter segregants.

Irregularities in segregation of vitamin-synthesizing abilities, and disturbances in mating type specificity were also encountered.

These experiments have yielded data that are not amenable to adequate interpretation on the bases of the established concepts of Mendelian genetics. Conversion of alleles in the heterozygote effected by gene-to-gene transfer of gene components has therefore been invoked as an explanation for the anomalies discovered.

LITERATURE CITED

Allen, C. F. (1930). Gametophytic inheritance in *Sphaerocarpus*. IV. Further studies on tuftedness and polyclady. Genetics **15**:150–188.

Brunswik, H. (1926). Die Reduktionsteilung bei den *Basidiomyzeten*. Zeitschr. f. Bot. **18**:481–498.

Burgeff, H. (1928). Variabilität, Vererbung und Mutation bei *Phycomyces Blakesleeanus*. Zeitschr. f. ind. Abst.-u. Vererbgsl. **49**:26–94.

Christensen, J. (1931). Studies on the genetics of *Ustilago zeae*. Phytopathol. Zeitschr. **4**:129–188.

Dickinson, S. (1928). Experiments on the physiology and genetics of the smut fungi. Cultural characters. I. Their permanence and segregation. Proc. Roy. Soc. Lond. B **103**:547–555.

Dimock, A. W. (1939). Studies on ascospore variants of *Hypomyces Ipomoeae*. Mycologia **31**:709–727.

Hanna, W. F. (1929). Studies in the physiology and cytology of *Ustilago zeae* and *Sorosporium reilianum*. Phytopath. **19**:415–442.

Kniep, H. (1928). Die Sexualität der niederen Pflanzen. Jena.

Lederberg, J. (1948). Problems in microbial genetics. Heredity **2**:145–198.

Lindegren, C. C. (1949). The Yeast Cell. Its Genetics and Cytology. Educational Publ. Inc. St. Louis.

————, (1949a). Chromosome maps of *Saccharomyces*. Hereditas Suppl. Vol., pp. 338–355.

————, and Lindegren, G. (1946). The cytogene theory. Cold Spring Harbor Symp. Quant. Biol. **11**:115–129.

————, ————, (1947). Depletion mutation in *Saccharomyces*. Proc. Nat. Acad. Sci. (U.S.) **33**:314–318.

Monod, J. (1947). The phenomenon of enzymatic adaptation. Growth Symp. **11**:223–289.

Mundkur, B. D., and Lindegren, C. C. (1949). An analysis of the phenomenon of long-term adaptation to galactose by *Saccharomyces*. (Amer. Jour. Bot., in press.)

Rodenhiser, H. A. (1932). Heterothallism and hybridization in *Sphacelotheca sorghi* and S. *cruenta*. Jour. Agr. Res. **45**:287–296.

Spiegelman, S. (1946). Nuclear and cytoplasmic factors controlling enzymatic constitution. Cold Spring Harbor Symp. Quant. Biol. **11**:256–277.

Stern, C. (1930). Konversionstheorie und Austauschtheorie. Biol. Zentralbl. **50**:608–624.

————, (1931). Zytologisch-genetische Untersuchungen als Beweise für die Morgansche Theorie des Faktorenaustauschs. *Ibid.* **51**:547–587.

————, (1932). Uber die Konversionstheorie. *Ibid.* **52**:367–379.

Winkler, H. (1930). Die Konversion der Gene. 186 pp. Jena.

————, (1932). Konversions-Theorie und Austausch-Theorie. Biol. Zentralbl. **52**:163–189.

Wülker, H. (1935). Untersuchungen über Tetradenaufspaltung bei *Neurospora sitophila* Shear et Dodge. Zeitschr. f. ind. Abst. - u. Vererbgsl. **59**:210–248.

Zickler, H. (1934). Genetische Untersuchungen an einem heterothallischen Askomyzeten (*Bombardia lunata* nov. spec.). Planta **22**:573–613.

EXPLANATION OF PLATE

PLATE I

Melibiose pour-plates of tetrad M532-M535. Three plates (left to right) have colonies each of which is individually capable of fermenting melibiose. Inocula derived from glucose slants corresponding to each clone can also ferment melibiose. Pour-plate of M535 has minute, non-fermenter colonies, and the clone derived from the corresponding glucose slant cannot ferment melibiose. The medium-sized colonies of M533 are not the result of crowding.
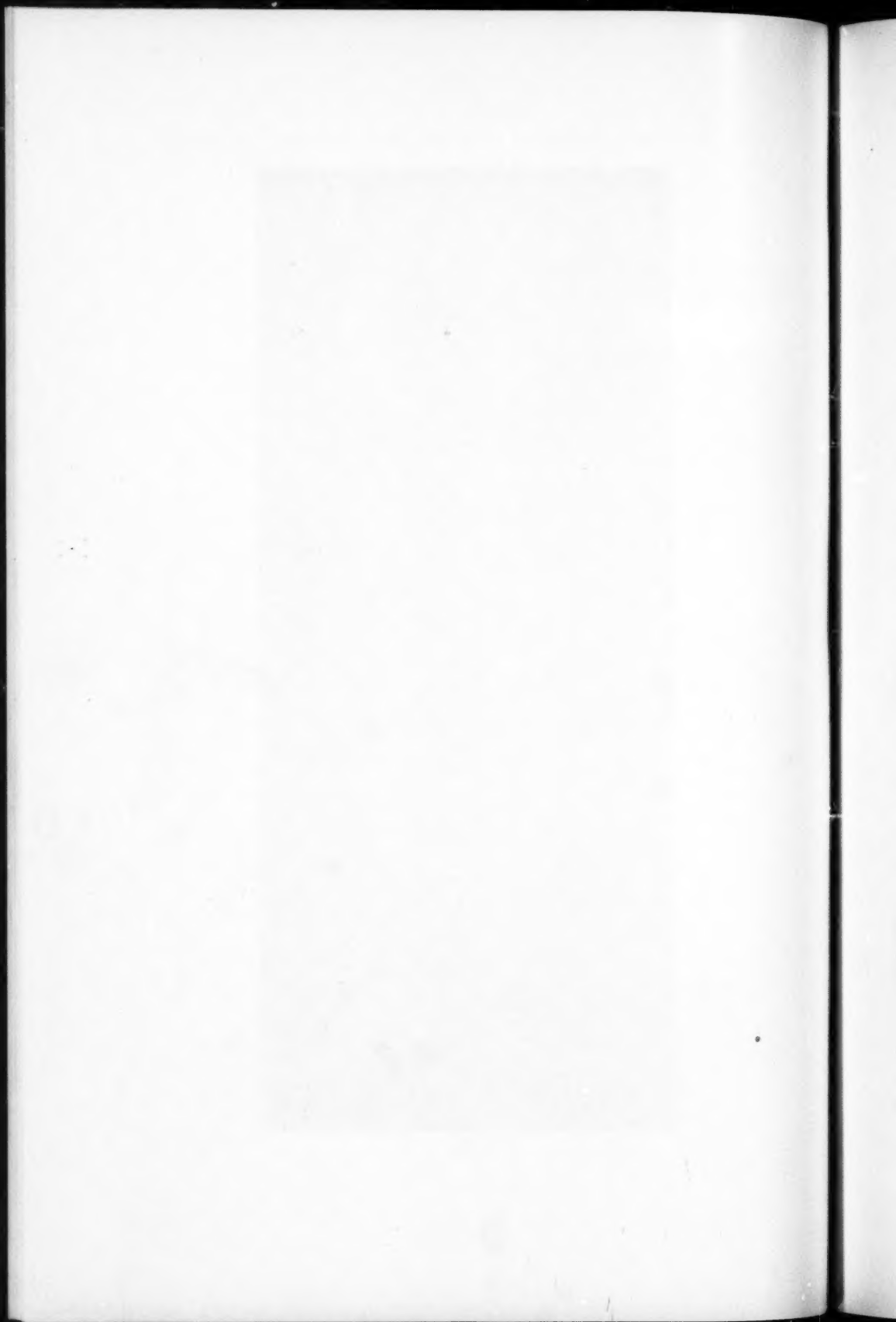
PLATE 1

M532

M533

M534

M535
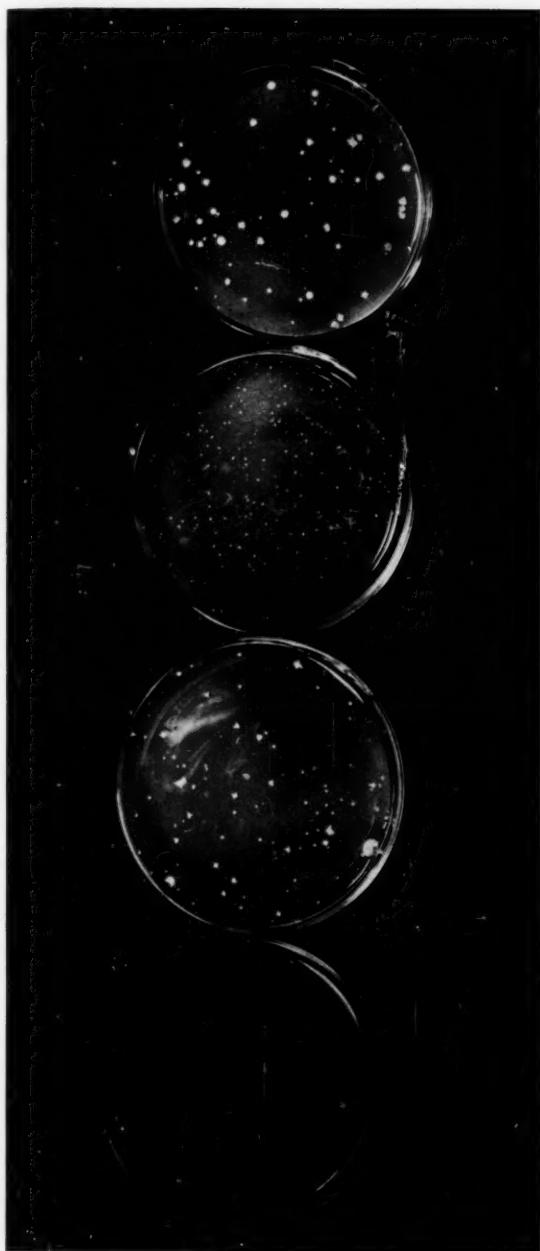
NEW SPECIES OF LONCHOCARPUS FROM PANAMA[1]

FREDERICK J. HERMANN

U. S. Department of Agriculture

Three Panamanian collections of *Lonchocarpus* which Dr. Robert Schery was unable to place among the species known from Central America were recently sent to the writer for study. All of them proved to be novelties for that region, as Dr. Schery had concluded: two of them undescribed species, of which the first is represented also in Costa Rica, and the third a tree of British Guiana, as follows:

LONCHOCARPUS oliganthus, sp. nov.—Frutex vel arbor gracilis ca. 10 m. alta; folia 5–7-foliolata; foliola oblonga vel elliptica multipunctata petiolulis subquadrangularibus; paniculae axillares 3–4 subspiciformes laxifloraeque foliis multo breviores; pedunculi secundarii minimi uniflori (raro biflori); pedicelli 0.5–0.7 mm. longi; flores 8–9 mm. longi, purpurei; calyx cupuliformis, margine integra vel aliquantum undulata; vexillum late oblongum vel oblongo-ovatum, externe dense argenteo-sericeum, margine valde inflexa; alae oblongae; carinae petala plus minusve falcata marginibus inferioribus solum per intervallum brevissimum apici propinquum connatis; stamen vexillare in fenestra et prope apicem columnae filamentarum liberum; ovarium 5–6-ovulatum; legumen ignotum.

Shrub or slender tree about 10 m. high, 17 cm. in diameter at base, with "dark brown, almost glabrous, shallowly striate bark" (Smith), and terete, glabrous, shallowly and irregularly sulcate branchlets dotted with small but conspicuous lenticels; stipules scale-like, oblong, 1 x 0.7 mm., dark brown, closely appressed; leaves 5–7-foliolate, 18–30 cm. long, the petiole subterete, canaliculate and often sulcate, glabrous or very sparingly strigose, 3.5–6.5 (averaging 4) cm. long, the rachis deeply canaliculate, sparsely strigose to glabrate; petiolules 4.5–6 mm. long, subquadrangular, minutely strigose to glabrous, dark brown to black, more or less canaliculate above; leaflets thin-chartaceous, oblong to elliptic, the blade 6–15 cm. long, 2.5–7 cm. wide, dark green (sometimes paler beneath), faintly but heavily mottled above with purplish brown, copiously strigose when young, at maturity glabrous or minutely and sparingly strigose beneath, multipunctate (each cell with several to many semitranslucent puncta), caudate at the apex, rounded or tapering at the base, the margin minutely crenulate, the lateral veins 9–10 pairs; panicles 3–4, borne singly in the upper leaf-axils, short (6–10 cm. long), much surpassed by the leaves, slender, subspiciform, loosely flowered; primary peduncles subterete to subquadrangular, glabrous or glabrate, slender (1 mm. or less wide at the base), floriferous to within 1.5–4 cm. of the base; secondary peduncles rudimentary, about 0.5 mm. long by 0.7–1 mm. wide, 1-, rarely 2-, flowered (the second flower commonly aborted); bracts and bractlets similar, squamiform, ovate, 0.7–1 mm.

long, densely strigose, the bracts caducous, the bractlets attached near the base of
the calyx; pedicels 0.5–0.7 mm. long; flowers 8–9 mm. long, "purple" (von
Wedel); calyx cupuliform, 2.5–3 x 3 mm., reddish brown, minutely tawny-
strigose, the margin entire or slightly undulate, the teeth, except the broadly
deltoid carinal tooth (0.1–0.4 mm. long), obsolete; standard broadly oblong to
oblong-obovate, 9 x 7 mm., reflexed, copiously silvery-sericeous without, glabrous
and lineate within, "center and margin pale green-yellow enclosing an area of
violet" (Smith), deeply emarginate and somewhat cucullate at the apex, the
margin strongly inflexed, irregularly truncate at the base, the auricles very short
(0.5 mm.), the claw 1.5 mm. long, a short (0.2 mm.) membranaceous crest
between each auricle and the claw; wings 9 mm. long (the claw 2.5 mm.), 2.5 mm.
wide, oblong, glabrous except for a sericeous median band (0.6 mm. wide), little
widened at the blunt apex, the vexillar half of the blade slightly prolonged at the
base to form a shallow auricle (0.7 mm.), adnate to the keel near the base; keel
petals 8.5 mm. long (the claw 2.5 mm.), averaging 2.5 mm. wide, somewhat
falcate, much broadened toward the blunt apex, their lower margins united only
at a point below the apex, glabrous except for the lower margin which is in-
creasingly sericeous toward the apex; stamens monadelphous, glabrous, the tube
fenestrate at the base with the margins of the opening thickened, the vexillar
stamen free at the opening (1 mm.) and also for the terminal 3 mm.; anthers
versatile but attached near the base, 2-celled, narrowly elliptic, 0.8 mm. long;
ovary compressed, linear, sessile or substipitate, densely white-strigose; ovules 5–6;
style strigose at base, glabrous above; stigma capitellate; pod unknown.

PANAMA: PROVINCIA DE BOCAS DEL TORO: Gray Creek, vicinity of Chiriquí Lagoon,
Sept. 8, 1941, *H. von Wedel 2634* (MO TYPE, US).

COSTA RICA: PROV. ALAJUELA: open shade in rain forest alt. 850 m., Villa Quesada,
San Carlos Canton, Feb. 21 1939, *Austin Smith H 1613* (F, MO).

The small, sericeous flowers of this species, together with the only slightly
coalescent keel petals, almost diadelphous androecium, narrowly oblong wings, and
inflexed standard, place it in the subdivision of NEUROSCAPHA designated by Pittier
as PUBIFLORI. Its nearest ally is *L. parviflorus* Benth., from which it differs in
having leaflets which are twice to three times as large, relatively long (6–10,
rather than 2.5 cm.), loosely flowered panicles, and larger flowers (8–9, rather
than 6, mm. long). The larger leaflets of *L. oliganthus* set it off likewise from the
related *L. atropurpureus* Benth., in which the pedicels are also occasionally, though
not predominantly, uniflorous, and from this it is further distinguished by having
petiolules twice as long, rudimentary secondary peduncles (0.5, rather than 2–3,
mm. long), narrower and densely sericeous standard with claw 1.5 instead of 0.8
mm. long, and densely pubescent ovary.

LONCHOCARPUS calcaratus, sp. nov.—Arbor 9 m. alta, ramulis crassis verru-
cosis; stipulae squamiformes, dense strigosae, caducae; folia 9–11-foliolata; foliola
subcoriacea, elliptico-lanceolata, epunctata, subtus strigosa; paniculae laterales, 25

cm. longae, axi primario florigeno simplici, valido, recto; axis secundarius 10–18 mm. longus, gracilis, 5–9 florus; pedicelli gracillimi, 5–6 mm. longi, bracteolis subulatis caducis strigosis prope basim calycis praediti; flores 16–17 mm. longi; calyx late cupuliformis vel cyathiformis, margine subintegra vel aliquantum undulata; vexillum orbiculare prope apicem emarginatum externe sparsissime sericeum; alae cymbiformes margine superiore basi leviter lobata; carinae petala oblongo-falcata ad basim lateraliter calcarata marginibus inferioribus vix connatis; stamen vexillare solum in fenestra columnae filamentarum liberum; ovarium 6–7-ovulatum; legumen ignotum.

Tree 9 m. high, with thick, subterete, often warty branches copiously marked with large, coarse lenticels; stipules squamiform, 2 mm. long, membranaceous, densely strigose, caducous; leaves 9- to 11-foliolate, 15–23 cm. long, the subterete petiole 2–5.5 cm. long, shallowly canaliculate, glabrous or glabrescent, the rachis sparsely strigose to glabrate; petiolules 3.5–5 mm. long, verrucose, conspicuously hirtellous, brown or occasionally olive-green, usually deeply but narrowly canaliculate above; leaflets subcoriaceous, elliptic-lanceolate, the blade 3.5–11 cm. long, 2–4 cm. wide, epunctate, glabrous or glabrescent above, strigose beneath, the apex obtuse, the base cuneate to abruptly acute, about 8–10 of the lateral veins prominent, not impressed, the margin entire, indurated; inflorescence lateral, paniculate, 25 cm. long; primary peduncle and rachis stout (3 mm. in diameter near the base), straight, unbranched, angular, very sparingly strigose, floriferous to within 3 cm. of the base; secondary peduncles 10–18 mm. long, slender, strigose, 5- to 9-flowered; bracts squamiform, 1 mm. long, densely strigose, promptly deciduous; pedicels very slender, 5–6 mm. long, strigose, the caducous copiously strigose bractlets subulate, 1 mm. long, attached near the base of the calyx; flowers 16–17 mm. long, "pink" (Allen); calyx broadly cupulate to cyathiform, firmly chartaceous, 3.5–4 x 8 mm., densely sericeous-strigose, the teeth prominent and broadly deltoid in the bud but the margin in anthesis subentire to shallowly undulate except for the apiculate (0.5 mm.) two lower teeth; standard orbicular, 15 x 15 mm., very sparingly sericeous without toward the emarginate apex, otherwise glabrous, the blade truncate to shallowly cordate at the base, the lobes almost obsolete, the cuneate claw covered by two inflexed, fleshy, partly adherent marginal flaps, their free edges meeting in the center; wings 16 mm. long (the claw 4.5 mm.), 7 mm. wide, cymbiform, very sparsely sericeous without toward the apex, adnate to the keel near the base, the vexillar margin abruptly rounded above the claw to form a broad, shallow lobe; keel petals 15 mm. long (the claw 5 mm.), 4 mm. wide, oblong-falcate, their lower margins united for a distance of 2.5 mm., 3.5 mm. below the obtuse to subacute apex, finely sericeous along the lower margin toward the apex, each petal bearing on its outer face an elongate (3 mm. long, 1.5 mm. wide), hollow spur or pocket midway between the margins, beginning 1 mm. forward from the claw; stamens monadelphous, the tube laterally compressed, fenestrate at the base, the vexillar stamen free only at the opening (2 mm.); anthers versatile but attached very near the base, 2-celled, ovate-oblong, 0.8 mm.

long; ovary linear, laterally compressed, densely white-strigose; ovules 6–7; style essentially glabrous; stigma capitellate; pod unknown.

PANAMA: PROV. DE COCLE: infrequent, El Valle, floor to 1800 ft., April 8, 1947, *Paul H. Allen 4472* (MO TYPE).

The prolonged, several-flowered secondary peduncles of this species in conjunction with epunctate leaflets allocate it in Bentham's section PANICULATI—a group otherwise unknown from Middle America but comprising a single species (*L. praecox* Benth.) in Minas Geraes, Brazil, and four species in tropical Africa. Although no material of any species of the section is available for study, it is evident from Bentham's descriptions (even though the 3-line characterization of *L. praecox* leaves much to be desired) that it is more closely related to the Brazilian species than it is to the African members of the section. The illustration of *Lonchocarpus praecox* in Martius' 'Flora Brasiliensis' (Vol. 15, pt. 1, *t. 105*. 1862) depicts a plant with much shorter panicles than those of *L. calcaratus*, much stouter and more prolonged secondary peduncles (these almost equalling the primary in diameter and length), smaller flowers with the calyx sparsely hirtellous and more prominently toothed, and elliptic-oblong, not at all lanceolate, leaflets. The resemblance of the present species is actually much closer to the plate in Martius (*t. 106*) designated as *Lonchocarpus glabrescens* Benth. The figure of the inflorescence in this plate presents a stout and elongated primary floral axis with short and very slender secondary peduncles as in *L. calcaratus*, but such a conspicuously paniculate inflorescence is not in agreement with Bentham's diagnosis (*"floribus fasciculatis"*) nor with modern collections from the valley of the Amazon which seem to be correctly referred to this species in the light of the original description. In these specimens the primary floral axis is decidedly woody with the characteristic rudimentary secondary peduncles of Bentham's section FASCICULATI to which he referred the plant. According to both Bentham's and modern accounts, *Lonchocarpus glabrescens* is, moreover, a liana with flowers having a subrostrate, strongly arcuate keel, usually 10 ovules, and more prominent calyx teeth.

The pronounced hollow spur in the carinal petals of *Lonchocarpus calcaratus* appears to be a feature almost unique in the genus, occurring otherwise, so far as the writer knows, only in *L. lineatus* Pittier of Gautemala. In the latter species the spur is much more shallow, and the two plants have few other characteristics in common.

LONCHOCARPUS DENSIFLORUS Benth.

A member of Bentham's section FASCICULATI, a group heretofore not known to be represented in Middle America. The possession of stipellate leaflets by *L. densiflorus* is an anomalous feature readily setting it off from other species.

PANAMA: PROVINCIA DE BOCAS DEL TORO: Laguna de Chiriqui and its neighborhood, Nov.–Dec., 1885, *John Hart 99* (US) (distributed as *L. sericeus*); Almirante, Sept. 12, 1920, *W. W. Rowlee & H. E. Stork 1002* (US) (distributed as *Andira* sp.). CANAL ZONE: vicinity of Mindi, Sept. 13, 1947, *Paul H. Allen 5119* (MO, NA).

A FIRST RECORD FOR THE GENUS QUALEA (VOCHYSIACEAE) FROM NORTH AMERICA (PANAMA)[1]

ROBERT W. SCHERY

QUALEA **cymulosa** Schery, n. sp.—Arbor 30 m. alta, ramis junioribus teretibus puberulentis, vetustioribus glabris cortice rimosa et longitudinaliter lenticellata, lenticellis numerosissimis fulvis elevatis; foliis simplicibus plerumque oppositis aut suboppositis aliquando alternatis, 10–15 cm. longis 4–6 cm. latis, integris ellipticis, ad apicem abrupte acuminatis, ad basim angustatis brevi-cordatis coriaceis glabris reticulatis inter nervos laterales; nervis lateralibus ca. 5–7 jugis arcuatis marginaliter confluentibus facere nervum costae parallelum 2–5 mm. ab margine, subtus nervis prominentibus; petiolis ca. 7 mm. longis, supra sulcatis, puberulentis fuscis; stipulis glandulis ovatis crateriformibus callosis ad petiolorum insertionem, duabus glandulis rotundatis inferius ad basin petioli decurrentis; inflorescentia 15 cm. longa 8 cm. lataque, terminali subterminalique, paniculis cymularum trichotomarum cinereo-puberulentis parvi-bracteatis vel subglandularibus; floribus magnis roseis, calcye cinereo-pubescenti coriaceo, 2 lobis lateralibus orbicularibus ca. 4–5 mm. longis, brunneis leviter pubescentibus, 2 lobis intermediis obovatis ca. 7 mm. longis, 1 loba interiora ca. 1 cm. longa, extus dense cinereo-pubescenti intus glabra, calcare bursiculato ca. 6 mm. longo ad basin inserto; petalo 1 obcordato glabro, ca. 2 cm. longo et 2.5 cm. lato apice profunde bilobato; stamine 1 crasso glabro, ca. 9 mm. longo, anthera biloculari; ovario rotundato dense cinereo-hirsuto 3-loculari, loculis biovulatis; fructibus ignotis.

Tall forest tree, the bark of the young (leaf-bearing) twig puberulent and scarcely lenticellate, the bark of the older twig glabrous and very lenticellate. Leaves simple, usually opposite or subopposite but sometimes alternate, glabrous, elliptic, rather abruptly acuminate, narrowed toward the base and briefly cordate at the extreme base, the lateral veins usually 5–7 pairs and confluent a few mm. from the margin into an undulate marginal vein subparallel to the prominent costa; petioles dark, puberulent, sulcate above; stipules apparently modified (at insertion of petiole) into crateriform "glands" with the elevated callous margins light in color, and with 2 smaller globose prominences a few mm. lower down to the side of the subdecurrent petiole. Inflorescence terminal but its lower subdivisions frequently axillary from upper leaves, thrice-compound, paniculate as a whole but the lateral branchings mostly trichotomous and determinate (cymose), bearing at its branches "glands" similar to the stipular ones, the ultimate and penultimate pedicels with small bracts. Flowers large, showy, rose-pink; calyx coriaceous, cinereous-pubescent, 5-parted, the outer (lateral) 2 lobes smaller, flat and lightly pubescent, the next inner 2 more or less coiled into a cylindric form, the innermost markedly curled into a cone-like cylinder about 1 cm. long, bearing at the base a broad but

flattened thick spur about 6 mm. long and 4 mm. broad, this rounded basally; petal solitary, obcordate, about 2 cm. long and 2.5 cm. broad, short-clawed at the base, deeply cleft at the apex, glabrous; stamen solitary, about 9 mm. long, glabrous, thickish, inserted to the side of the petal, bearing terminally a large, fleshy, bilocular anther less than 2 mm. long; ovary densely cinereous-hirsute, completely 3-carpellate, each carpel 2-ovulate; style glabrous, about equalling the stamen; stigma prominent, capitate.

PANAMA: DARIEN: headwaters of the Río Chico, June 1947, P. H. *Allen 4645* (Mo. Bot. Gard. TYPE).

This new species constitutes the first record of the genus north of South America. It is thus another example of a typically Amazonian plant having a northern range extension into the dense forest of eastern (southern) Panama. The species apparently falls into Warming's section COSTATAE (Fl. Bras.) of the genus, and as far as can be told from the literature is distinct from all of the multitude of Amazonian species. There is nothing even similar to it in the relatively meager collections of *Qualea* in the herbarium of the Missouri Botanical Garden, but it may resemble certain Brazilian species such as *Q. rupicola* Ducke, to judge from the original description only.

SOME PTERIDOSPERM STEMS AND FRUCTIFICATIONS WITH PARTICULAR REFERENCE TO THE MEDULLOSAE[1]

ROBERT W. BAXTER[2]

INTRODUCTION

Theophrastus, one of the first to attempt the classification of plants, recognized as his major groups, trees, shrubs, and herbs. Although this division was long ago realized to be an artificial one it nevertheless provided then, as it does today, convenient categories for different types of plant habit. Since the study of paleobotany involves not only the search for the ancestral types of present-day plants but also attempts to visualize and illustrate the gross appearance of past floras we may still find it convenient to use these major habit groupings in classifying fossil plants.

We now know that the Carboniferous forests were made up of the tree-like *Pitys, Cordaites, Lepidodendron, Sigillaria* and *Calamites,* which attained diameters of several feet and reached 100 feet or more in height. Growing among these trees were numerous plants of creeping, climbing, and shrubby habit, characterized in general by small stems with little or no secondary growth. It is also generally true that this last group (ferns and seed-ferns) had developed large leaves or fronds (megaphyllous) while the larger tree-like plants were generally small-leaved (microphyllous). The term "microphyllous" is used in this paper in a broad sense to include not only the groups lacking leaf gaps but also those living and fossil gymnosperms (Coniferophyta, Arnold, 1948) in which the seeds are stem-borne (Sahni's (1920) Stachysperms) and the leaves are small, simple, linear or fan-shaped growths, borne in dense spirals or whorls on the trunk and branches.

In plant evolution the early development of a single large trunk (tree-like) seems to have some correlation with microphyllous habit, as the development of numerous small branches of equal size (shrubby) may be correlated with megaphyllous form. Accordingly, it seems possible that a classification based on external form and size may, considered in relation to the origin of plant groups, not be entirely without some phylogenetic meaning.[3] As might be supposed, the larger tree-like fossils

---

[3] While it is not our present intention more than to suggest the possibility of the foregoing statements, there is ample evidence that the Coniferophyta (Ginkgoales, Taxales and Coniferales) have been trees and microphyllous since their origin from the Pityeae and Cordaiteae in Upper Devonian and Carboniferous times (Arnold, 1948). The other groups of Carboniferous trees *(Calamites, Lepidodendron,* etc.) are, on the other hand, represented today by only a few isolated genera in the so-called fern allies. Thus it would seem that the only possible ancestral forms of the megaphyllous gymnosperms, and possibly the angiosperms, must be sought in the shrubby, climbing or herbaceous undergrowth of the Paleozoic forests. In this habit group through profuse equivalent stem ramifications the *telome* units would be provided for the development of the large frond and broad leaf, which when fertile may have evolved into sporophylls or carpels (Wilson, 1942).

have received a proportionate amount of attention and are today relatively well known.   On the other hand, while numerous genera and species of the smaller plants have been discovered and described, it is becoming increasingly apparent that the field is open for the discovery of many more.   This is due in part to improved techniques and increasing amounts of research material but probably even more to the undoubted greater diversity of the smaller plants.   Certainly in many forest areas today, the genera and species of tree-like habit are but a small fraction of the total flora as compared to those of associated shrubs and herbs.   In the present paper we intend to deal with some of these newly discovered small plants (or plant organs) which appear to be of pteridosperm affinity.

As is well known to all paleobotanists, the fragmentary nature of the material preserved in coal balls makes it necessary to describe the isolated plant organs (stems, roots, leaves, fructifications, etc.), with the hope that subsequent work will show their proper assemblage.   Thus the seed-ferns as a group were originally described as the Cycadofilicales on the basis of stem anatomy, which seemed to combine both fern and cycad characters along with a constant association with fern-like foliage.   It was not until 1905 that seeds were actually found attached to some of these fronds and the present conception of the groups was created.   Even now the possession of seeds is definitely known for only the genus *Lyginopteris* (*Calymmatotheca Hoeninghausi*) and can only be inferred for the numerous other stems which have been carried over into the new classification on the basis of their similar anatomy.   Briefly, the characters on which this relationship is based are: small stems, pith or mixed protostele with exarch or mesarch primary wood, secondary wood of characteristic angular (in cross-section) tracheids, reticulate-bordered pitting, usually numerous leaf traces, and an outer cortex containing vertical or horizontal sclerotic bands.   Additional similarities and differences are shown in the accompanying table which lists most of the better-known pteridosperm stem genera.

Our new genus (page 289) is validly included through possession of most of the above-listed characters although it lacked leaves and may or may not have had seeds.   Its reconstructed habit (plate 5) does, however, show a close flattened branching pattern which offers implications as to the possible megaphyllous development of large fern-like fronds.   Such ramification in a single plane, along with the lack of leaves, is suggestive of the Psilophytales, and it is our opinion that *Microspermopteris* may constitute a direct link between that primitive group and the larger seed-ferns.   The constant small size (5 mm. or less) of its stems indicates that it would at best have been an inconspicuous element of the forest group and must have been either prostrate or climbing.

The three new species of *Medullosa* described are of course generically identifiable by their polystelic structure as well as by the character of the wood and pitting and, where the latter tissue is preserved, by the fibrous cortex.   Here again the evidence of size and form seems to indicate that the habit was either creeping or climbing rather than tree-like.

The two new species of *Dolerotheca* are offered primarily as a supplement to Schopf's (1948) comprehensive work on the genus, although we believe our material does present some basis for additional phylogenetic interpretation as well as possible additional support for the more definite connection of the fructification to the Medullosae.

During the latter course of this study several additional small stems of apparently primitive pteridosperm character have been discovered which we hope to describe in a future paper. One in particular is of interest since, as in *Microspermopteris,* it appears to be leafless. Thus at least a part of the undergrowth of Carboniferous times seems to have occupied a position comparable to that of the living fern allies in that both present a retention of characters primitive for their time so that the excellent fossil record of the coal beds may yet provide the missing links from earlier eras just as those primitive living genera *(Lycopodium, Equisetum* and *Psilotum)* have done in part for the present-day flora.

Microspermopteris aphyllum, gen. et spec. nov.

The following description is based on a total of eight stems occurring in three different coal balls. Four stems were followed through one coal ball for approximately 6 cm. and three stems extended through another ball for approximately 4 cm. The eighth stem was isolated in the third coal ball and was cut as a longitudinal section 1 cm. in length.

All material is from the What Cheer Clay Products Co. coal mine, one-half mile west of What Cheer, Iowa. This horizon lies in the Des Moines series of the Pennsylvanian and is accordingly of Upper Carboniferous age.

The stems followed a relatively straight to slightly sinuous course. Mixed among them were numerous specimens of their smaller, but otherwise identical branches.   The stems are of a constant small size even when maturity is indicated by considerable secondary growth. The total diameter including cortex and epidermal tissues never exceeds 5 mm., while the single stele averages 2 to 2½ mm.

The external form of the stems is quite variable, particularly in the smaller specimens where the transverse configuration is almost "amoeboid" in outline (fig. 3). The more mature specimens with considerable secondary growth appear oval to circular in cross-section (figs. 1 and 7).

The primary tissues consist of a protostele in which the large metaxylem tracheids are divided into groups of 12–14 cells by a radiating network of parenchyma, the individual strands of which are usually not more than one cell in thickness and in longitudinal section are seen to be vertically elongated cells, five to six times as long as wide. The inconspicuous protoxylem groups are situated on the periphery of the primary tissue and appear to be exarch though their exact position is vague due to the very small size of the adjacent innermost secondary wood. The metaxylem tracheids increase slightly in size towards the center, averaging 150 μ in diameter as against 50 μ for the secondary wood. All walls of the metaxylem are reticulately bordered pitted with the opposing orifices at a slight angle to one another (fig. 12).

Comparative characters of seed-fern stem genera	Approximate number of steles and stem diameter	Primary wood	Secondary wood and ray structure	Cortex	Leaf traces and petiole	Horizon
Microspermopteris	Single stele Stem: 5 mm.	Exarch; a nearly solid to mixed protostele divided into groups of 12–14 cells by parenchyma network	Secondary wood usually well developed, increasing in size towards outer layers; pitting reticulate-bordered. Rays few, low, uniseriate.	2-zoned; inner zone homogeneous; outer zone with a vertical series of horizontal sclerotic plates	Leaf traces lacking; branch traces concentric and identical to stele; branching at right angles to stem	Des Moines Series, Pennsylvanian
Lyginopteris	Single stele Stem: 2–4 cm.	Relatively large pith; sclerotic nests with marginal strands of mesarch primary wood	Secondary wood often well developed, interrupted by leaf traces. Rays wedge-shaped, wider towards outside	Inner cortex with sclerotic nests and secretory cells. Outer cortex with anastomosing vertical sclerotic bands; spinous emergences	Leaf traces originate in primary wood on pith margin and pass out through gaps in secondary wood; divide into 2 in cortex and fuse V-shaped in petiole	Carboniferous
Heterangium	Single stele Stem: 1–2 cm.	A mixed protostele, usually mesarch	Secondary wood seldom more than 8–10 layers thick; reticulate-bordered pitting. Rays broad, often wedge-shaped	2-zoned; inner zone with horizontal sclerotic bands; outer zone with vertical sclerotic bands	Leaf traces originate as 1 or 2; always dividing into 4–8 in the petiole	Lower Carboniferous to Permian
Rhetinangium	Single stele Stem: 2 cm.	Exarch; a mixed protostele with very large metaxylem cells and parenchyma with secretory cells	Secondary wood with reticulate-bordered pits on radial walls. Rays broad and high	Inner cortex lacking sclerotic tissue; outer cortex with vertical sclerotic bands	4–5 U-shaped traces with exarch protoxylem form a single corrugated band. Petiole base larger than main stem	Lower Carboniferous
Medullosa	2–8 steles Stems: 2–12 cm. (excl. Permian species)	A mixed protostele with large metaxylem cells. Protoxylem usually exarch	Secondary wood usually with greatest growth towards stem center. Rays thin (1–2 cells) and 1 cm. or more high	Containing numerous collateral leaf traces and resin canals; outer cortex with vertical sclerotic bands	Leaf traces collateral, very numerous. Petioles large with numerous traces	Lower Carboniferous to Permian

Comparative characters of seed-fern stem genera	Approximate number of steles and stem diameter	Primary wood	Secondary wood and ray structure	Cortex	Leaf traces and petiole	Horizon
Sutcliffia	1 large central stele surrounded by small subsidiary strands (meristeles) Stem: 12 cm.	Exarch; a mixed protostele with large metaxylem cells and parenchyma with secretory cells	Secondary wood weakly developed (3–4 rows). Rays thin (1–4 cells), 1–2 cm. high	Outer cortex with vertical sclerotic bands similar to *Medullosa*	Traces concentric, numerous, arising from meristeles. Petioles similar to those of *Medullosa*	Lower Carboniferous
Stenomyelon	Single stele Stem: 2 cm.	Triangular mixed protostele; parenchyma bands running from 3 corners to center	Secondary wood well developed; reticulate-bordered pitting on radial walls. Rays broad and wedge-shaped	Inner cortex lacks sclerotic tissue; outer cortex with vertical sclerotic bands	Leaf traces originate from corners of triangular protostele and divide into numerous bundles	Late Devonian and Lower Carboniferous
Calamopitys	Single stele Stem: 2–5 cm.	A pith with endarch primary xylem or a mixed protostele	Secondary wood often well developed (20–30 rows); reticulate-bordered pitting on radial walls. Rays broad	Outer cortex with vertical sclerotic bands similar to *Medullosa*	Leaf traces often concentric, leave stele as 1 or 2 and divide into 6–8 or more in the petiole which resembles that of *Medullosa*	Late Devonian and Carboniferous
Aneurophyton (*Eospermopteris*, (see footnote, p. 294)	Single stele Stem: 1–2 cm., although 3-ft. stump casts are recorded	Triangular protostele, exarch with proto-xylem at the 3 angles	Abundant secondary wood; reticulate-bordered pits on radial and tangential walls. Rays small, thin, 1–2 cells wide	Outer cortex with scattered vertical sclerotic strands	Leaf traces lacking; branch traces similar to main stele but smaller	Middle Devonian
Schopfiastrum	Single stele Stem: 2 cm.	Exarch; a mixed protostele	Secondary wood well developed; reticulate-bordered pits on radial walls. Rays thin and high	Resin canals rare or absent; outer cortex with vertical sclerotic bands	Leaf traces large, bilobed, in opposite pairs	Des Moines Series, Pennsylvanian

The secondary wood ranges from 3–4 rows in thickness in the young small stems to around 16 in the larger more mature specimens. The first-formed cells are quite small, being hardly distinguishable in size from the protoxylem. Their diameter increases gradually towards the outside but never approaches that of the metaxylem. Longitudinal sections of the secondary tissue show the radial walls pitted in the same way as the metaxylem, with a dense reticulum of bordered pits, while the tangential walls have fewer scattered pits, with more lineal openings, arranged in irregular rows up and down the central area. Wood rays are inconspicuous and relatively sparse. They are small, uniseriate and from 1 to 4 cells in height (fig. 9). A rather frequently observed character of the secondary wood of the mature stems is its unequal development (fig. 7) which is possibly due in some cases to differing cambial activity and in others represents the unfilled gaps left by departing branch steles. The tissues immediately surrounding the wood are seldom well preserved and are represented in all of our specimens as merely a thin dark brown ring of crushed cells. There is no evidence of periderm formation.

The cortex is divided into an inner and outer zone of approximately equal thickness. The inner part is composed of poorly preserved isodiametric thin-walled cells containing numerous, scattered dark secretory cells. The outer zone is thicker-walled and usually better preserved, consisting of a compact tissue of brick-like cells (hexagonal to circular in transverse section), about twice as long as wide, the elongation being parallel to the axis of the stem. This merges into an outermost tissue which is 2–3 cells thick and differentiated by being made up of cells four to six times as long as broad. An unusual character of this tissue is the frequent occurrence of multicellular emergences which are commonly broad at the base, tapering to a sharp point. They are sometimes forked and horn-like (figs. 5 and 55) and may occur singly or in clusters (fig. 8). In length they average .6 mm. There is no evidence that they were glandular like the emergences of *Lyginopteris*, nor do they appear to have been arranged in parallel rows as has been described for the latter genus (Scott, 1923). On the contrary, they are produced more or less indiscriminately with the exception that they are nearly always present at the point of departure of a branch.

A feature of the outer cortical zone which is probably the most unique in relation to the comparable pteridosperm genera is the presence of a vertical series of *horizontally* aligned sclerotic plates instead of the usual vertical strands. These consist of thick-walled stone cells, 2–4 cells deep and 4–6 cells in diameter (fig. 10). In tangential section they are occasionally seen to anastomose with adjoining plates at the same level and with plates above and below, thus appearing as a loosely arranged horizontal network (fig. 11).

One of the most difficult problems in interpretation has been the question of whether *Microspermopteris* bore leaves. As stated earlier, we have followed four of the stems for approximately 6 cm., three for 4 cm., and another for about 1 cm.

This produced a close check on nearly 37 cm. of stem, all, of course, not of the same plant. However in this rather respectable amount of material we encountered only five instances of vascular tissue being given off from the main stele. In every case the details are identical and are illustrated for both a young and mature specimen in figs. 1, 2, 3, 5 and 55.

The branch is first evident as a departure from the stele of a complete segment of primary and secondary wood, with the crushed phloem and cambium tissues on its outer, abaxial surface. At this point it consists of 8 to 12 metaxylem cells with possibly 1 to 2 strands of protoxylem, bordered on the outer side by almost the complete amount of secondary wood present at that particular point on the main stele. This results in a conspicuous gap being produced in the mature stems and a relatively smaller one in the young stems where the proportion of secondary growth is much less. The angle of departure is acute (around 30°), the trace following this steep course through the cortex for approximately 2 to 3 mm. During this space the secondary wood and enclosing parenchyma tissues completely surround the primary core and produce a concentric bundle identical to the main stele except in size. The bundle then turns sharply outwards and proceeds at right angles to the stem axis for a distance approximately equal to the normal diameter of the stem before again resuming an upward course. As shown in fig. 5, the branch, where it projects horizontally out from the stem, almost equals the stem in size and exhibits all of its characteristic sclerotic plates and cortical zones. At no time does the bundle show any tendency to subdivide further, while a transverse section of one of the branches at a point around 4 mm. from the main stem shows it initiating a further small branch of its own in the same plane as the primary one. The branching was apparently distichous at relatively long intervals, so that the habit was probably fairly close to the partial reconstruction shown in pl. 5.

Adventitious roots, which are primarily limited to the axis of the branches, are similar to those of *Lyginopteris*. They are commonly hexarch or heptarch with conspicuous protoxylem groups at the points of the projecting arms (fig. 4). The phloem lies between these arms and, as in *Kaloxylon*, there is a small amount of conjunctive parenchyma in the metaxylem. The stele is enclosed by a single poorly preserved dark ring which probably represents the endodermis. The cortex is homogeneous and identical to the inner cortical zone of the stem. The peripheral zone is undifferentiated, so that in transverse section the loosely packed cortical tissue with scattered secretory cells appears to extend clear to the edge of the irregularly lobed outer margin. This lack of a differentiated epidermal zone is one of the distinguishing features between these roots and those of *Lyginopteris*.[1] Secondary growth is rather rare but when present is again similar to that of *Kaloxylon*, cambial activity initiating in the depressions between the protoxylem

---

[1] While the information in the literature is often vague on this point, similar roots have also been described for *Heterangium*, although they are usually listed as diarch or triarch (Scott, 1923).

points and producing wedges of typical secondary wood alternating with wedge-shaped rays opposite the protoxylem. The pitting is identical to that of the corresponding tissues in the stem. As might be expected, the roots are of constant small size, with the most mature specimens showing 6–7 layers of secondary growth not exceeding 2 mm. in total diameter. The point of their insertion on the stem offers another similarity to *Kaloxylon* as roots are most frequently found immediately above the branch attachment (see Scott, 1923, p. 49) where their horizontally departing bundle seems to function, in part, in filling up the branch gap. As it has been possible to follow these roots from their insertion on the stem (fig. 6) out to typical transverse sections as in fig. 56, their identity is beyond doubt.

Discussion:

At first glance, in transverse view *Microspermopteris* presents a close resemblance to *Heterangium*. The size is comparable to *H. minimum* (Scott, 1917), and the primary wood with its thin network of parenchyma separating large groups of tracheids is more closely approximated by *H. Kukuki* (Hirmer, 1933) although the total amount of parenchyma is much less in *Microspermopteris*. In the anatomy and insertion of the roots and the presence of multicellular emergences on the stem and branches we have structures comparable to *Lyginopteris*. However, the almost solid protostele contrasts with that of *Lyginopteris*, while the absence of leaf traces and of a vertical fibrous hypoderma, along with the exarch position of the protoxylem, removes all possibility of assigning the specimens to *Heterangium*.

While the horizon of our petrifactions is late Upper Carboniferous and *H. Grievii* Scott is of Lower Carboniferous age, there seems little doubt but that we are dealing with a more primitive plant which possibly represents the ancestral stock of *Heterangium*. In fact, if it were possible to increase slightly the amount of parenchyma in the primary wood, fuse (through webbing) the closely grouped parallel branches into a multi-bundle rachis (Lignier's (1908) theory of megaphyllous development), and add a hypodermal zone of vertically elongated fiber bands we would have a stem quite similar to *Heterangium*. The sclerotic plates lying in the extreme outer cortical zone of *Microspermopteris* (fig. 10) are in radial view somewhat similar to the plates found in the middle cortex of all of the *Heterangium* species (with the exception of *H. minimum* which, according to Scott, lacks fibrous and sclerotic tissue altogether).

The most obviously primitive and unusual feature, the leafless condition, can be assumed to be demonstrated since our material permitted examination of approximately 37 cm. of different stems. The only similar character in plants of possible pteridosperm affinities is in *Eospermopteris (Aneurophyton)* of the middle Devonian.[1] We must assume, then, partly on the lack of any intervening evidence, that we are dealing with a link leading the pteridosperm complex clear back to the

---

[1] Although the fructifications originally described as seeds were later shown to be sporangia the anatomy of the stem still provides some basis for including the genus in the pteridosperms.

Psilophytales. Indeed, Dawson's restoration of *Psilophyton princeps* (known only from compressions) is disturbingly similar to our own restoration of *Microspermopteris*, particularly in the flattened branching pattern and the presence of spine-like emergences on the stem. Since what we know of *Psilophyton* stelar structure indicates that it possessed only spiral and scalariform pitting there obviously cannot be any direct comparison in internal anatomy with that of the secondary wood and highly developed bordered pitting of *Microspermopteris*. However, the gross appearance is close enough to intimate that a compression form of *M. aphyllum* might be identified as a *Psilophyton*. The middle Devonian genus *Schizopodium* offers a closer parallel in pitting and beginning of secondary growth. However, we consider it here just an example of the early, contemporaneous origin of these characters in contrast to the more conventionally primitive scalariform pits and solitary primary tissues, since the present evidence indicates its relationship to the Cladoxylaceae rather than the Pteridospermae.

In Andrews' (1940) account of the stelar anatomy of the pteridosperms he makes the following observation:

> . . . it should be stated that the view that the pteridosperms represent an intermediate group between the ferns and cycads is no longer tenable. Rather we must look to a common psilophytalean-like ancestor with terminally borne sporangia, a solid protostele and primitive secondary wood for the origin of the ferns and pteridosperms . . .

While we are more inclined to feel that the ferns arose independently, in many ways our present genus fulfils the theoretical requirements outlined.

The possibility that *M. aphyllum* was parasitic and its leafless condition a result of degeneracy rather than primitiveness has not been overlooked. The fact that the habit was probably epiphytic (climbing) or prostrate in a swamp humus tends to lend some weight to such a view as does the apparent absence of stomata and potential photosynthetic tissues. However, since no organs resembling haustoria are present and the roots resemble so closely the aerial ones of *Lyginopteris* we cannot consider a parasitic condition too seriously. At the same time the combination of so many characters common to both *Lyginopteris* and *Heterangium*, along with the more primitive stelar structure and lack of differentiation into rachis and lamina, seems to point rather definitely to an ancestral form from which both genera may have developed independently. This conflicts with Scott's (1923) theory of *Lyginopteris* arising from a developmental series through the subgenus *Lyginangium*, and it may be necessary to reconsider some of Kubart's transitional *Heterangium* species as being actually primitive *Lyginopteris* species leading back to *Microspermopteris*.

Since no seeds or any fertile parts whatever have been found, it is necessary to include *Microspermopteris* among the numerous other organ genera assigned to the seed-ferns on purely anatomical characters. It may be open to question whether in its leafless condition it could have borne seeds. If they were present they were

more than likely terminal on the smallest branch divisions. However, there is no reason for not considering the possibility that the stem anatomy constituting the organ genera of pteridosperms did not precede the development of seeds (i.e. *Eospermopteris (Aneurophyton)*. Certainly in many of the Devonian and Lower Carboniferous Calamopityaceae the presence of seeds is still to be proven, although the degree of differentiation into stem and leaf-bearing organs had obviously reached a more advanced stage than that shown by *Microspermopteris*.

It can be hypothesized that certain small psilophytalian plants struggling for survival in an environment of increasing lushness and density might well have developed a vine-like habit, involving additional conductive stelar tissue as well as supporting sclerotic and fibrous zones, to be followed chronologically by differentiation into leaves (as a more efficient light-catching mechanism) and still later by seeds as a product of the changing and possibly drying environment. Viewing evolutionary change as a response to environmental change, it is difficult to see seed production ever replacing reproduction by spores if there had not been a constant impetus to survival under conditions unfavorable (lack of proper moisture) to spore germination. It also seems likely that the struggle for living space and light preceded the above conditions.

From the original psilophytalian stock larger and anatomically more complex forms would arise independently, leading by gradual ecological adaptations to the recognized groups of Carboniferous plants. Certainly, the contemperaneous association, even as early as the Upper Devonian period, of widely differing stelar structures for the ferns and pteridosperms would seem to indicate that they had a separate individual origin. Some of the earliest known forms assigned to the ferns such as *Arachnoxylon* and *Reimannia* of the Upper-Middle Devonian show definite affinities to the Carboniferous Zygopteroideae, while *Eospermopteris* of about the same age shows many seed-fern characters *in spite of apparently producing only spores*. Thus, although the picture is complicated by the existence of numerous genera from compressions of which we have no knowledge of the internal anatomy (i.e. *Archeopteris*, etc.), the safest and most consistent distinction between the two groups would seem to be stelar structure. Using this as a criterion, it would be possible to have a phylogenetically correct classification including, on the one side, pteridosperms, having only terminal sporangia and, on the other side, ferns exhibiting heterospory. There certainly can be no reasonable objection to recognizing that the seed-ferns must have passed through a sporangiate stage or that ferns may not have achieved heterospory as a terminal development rather than as a stage in seed production.

The designation of the group as Pteridospermae becomes increasingly unfortunate if we recognize their independent origin from the Psilophytales and the fact that the most primitive genera undoubtedly lacked seeds. The same situation has

been dealt with in the Lepidodendrales (i.e. *Lepidocarpon* vs. *Lepidostrobus*) with much less confusion. Here the general plant structure and anatomy have been accepted as the basis for the order, while seed production has been recognized as an advanced stage of heterospory within certain species and genera. For some reason it has never seemed necessary to create the Lycopsidospermae to include *Lepidocarpon* although considered on the same basis as the pteridosperms such should be the case.

The following seem to the author to be the important points to bear in mind in relation to Pteridospermae in question.

(1). They are psilophytalian in origin rather than arising from the ferns.

(2). They are possibly of dual origin, with *Eospermopteris* leading to the Calamopityaceae complex and *Microspermopteris* leading to the *Lyginopteris* and *Medullosa* complex.

(3). Leaves *when present* are large and fern-like; seeds *when present* are basically terminal.

(4). The stem and petiole anatomy is constant and characteristic enough to delimit clearly the group irrespective of known possession of seeds.

(5). Included on the basis of the above anatomical criteria are genera such as *Microspermopteris*, which may or may not have had seeds, and *Eospermopteris*, in which the possession of seeds seems doubtful.

(6). While genera known only from compressions such as *Archeopteris* may be links in the pteridosperm chain, they are just as likely, in the absence of anatomical evidence, to be true ferns. Heterospory, as shown by the modern genera *Salvinia* and *Marsilia*, as well as the fossil lycopods, does not necessarily always imply later seed development.

(7). Seed development in the pteridosperms may in some isolated cases have preceded the differentiation of fern-like leaves with the seeds being borne terminally on naked branches. In other words, we are possibly dealing with early seed-plants which through parallel evolution developed fern-like leaves rather than, as originally thought, with ferns which developed seeds. The distinction may seem trivial, but while the original premises are close the phylogenetic conclusions (depending on which starting point is selected) are quite distinct. The terminal position of the seed in *Lyginopteris oldhamia* and *Aneimites fertilis* are cases in point since these species are among the oldest forms in which seeds are known.[1] (We can only hope that the discovery of fertile material of *Microspermopteris* will illuminate this point.)

Diagnosis:

Stems of constant small size, the stele never exceeding 2.5 mm. or the entire stem 5 mm. *Metaxylem* of large cells (150 μ diameter), diminishing towards the

---

[1] While these seeds are "terminal" on leafy fronds rather than on naked stems it seems not unlikely that their apical position involves a carry-over from a developmental stage prior to the acquisition of leaves.

periphery. Protoxylem exarch, of numerous indistinct groups. Xylem parenchyma arranged in a thin network enclosing groups of 12 to 14 metaxylem cells. *Secondary wood* of small angular (in cross-section) tracheids from 3 to 16 layers in thickness, increasing in size towards the outer edge. Reticulate-bordered pitting with crossed orifices in the metaxylem and on radial walls of the secondary wood. Scattered bordered pits with lineal openings on tangential walls. Protoxylem spiral or annular. Rays rare or lacking; when present, small, uniseriate, 1–4 cells high. *Cortex* differentiated into inner and outer zones. The inner zone composed of isodiametric thin-walled cells, poorly preserved, with scattered secretory cells but lacking sclerotic tissue. Outer zone of thicker-walled, longer cells containing vertical series of horizontal sclerotic plates. *Epidermis* of similar but more elongated cells producing numerous multicellular pointed emergences. *Leaf traces* lacking. Branching distichous and at right angles to the stem. *Roots* adventitious, hexarch to heptarch, commonly inserted above point of branch departure.

Horizon: Des Moines Series of Pennsylvanian.

Type: fig. 1. Slide 1602 in the paleobotanical collection of the Henry Shaw School of Botany of Washington University.

SOME NEW AMERICAN MEDULLOSAS

In the interval since Thiessen (1920a, 1920b) discovered and identified a pteridosperm stem as *M. anglica* (later to be assigned varietal distinction by Schopf, 1939) three new species and one variety of *Medullosa* from American coal balls have been brought to light. They are: *M. Noei* (Steidtmann, 1937), *M. distelica* (Schopf, 1939), *M. Thompsonii* (Andrews, 1945), and *M. anglica* var. *ioensis* (Andrews & Kernen, 1946). With the exception of *M. Noei* all of these new species and varieties have formed a fairly closely integrated group assignable to the subgenus Anglorota along with the European species *M. anglica*, *M. centrofilis*, and *M. pusilla*. *M. Noei*, showing affinities with *M. Leuckarti*, is held to be transitional between the Carboniferous form cycle and the Permian species.

Our knowledge of this very interesting group has been expanding rather rapidly, and with the hope of throwing still further light on the subject three new species of *Medullosa* are herewith described and additional new data are presented on *M. Noei*.

Medullosa primaeva, sp. nov.:

The following description is based on a single coal ball specimen from the Urbandale Mine located 1.2 miles west of Des Moines, Iowa, on U. S. Highway No. 6. This is the same location from which Andrews (1945) described *M. Thompsonii*. The horizon is the Des Moines Series of the Pennsylvanian. The material was collected and cut by Mr. Frederick O. Thompson of Des Moines, who generously donated it to the Henry Shaw School of Botany of Washington University. It consists of a cut block 5.5 x 5.5 cm. and 1.3 cm. thick, with the stem

exposed on one side through a fracturing away of the adjoining material. The stem's course is through the thickness of the block at a slight angle from the vertical, the total available length being 1.4 cm. Figures 14 and 15 show the appearance of the top and bottom surfaces of the specimen prior to any grinding of the fractured edge. Approximately one half of the cortex and external tissues have been lost on the side of the fracture, though the multiple stele appears to be nearly intact.

As shown in fig. 14, the upper[1] surface of M. *primaeva* exhibits 5 rather large and uniform-sized steles, 2 of them partially fused. There are also 2 small steles and a portion of a third on the fractured margin. The lower surface shows the same 8 steles, though somewhat altered in orientation and size, with 3 of the steles partially fused. It is not implied, however, that 8 was the constant number of steles as even in the short length of stem available stelar fusions and divisions were numerous and the diversity of vascular growth even included the production of steles running horizontally through the stem for short distances (fig. 13). Still, even with these variations the stele number seems to have been constantly 6 or more.

The stem measures 2.0 cm. in diameter, the individual steles ranging from around 5 mm. for the average large ones to .5 mm. for the very smallest. The 5 largest steles are closely comparable in size to those of M. *Thompsonii* even though the stem of the latter is considerably larger, averaging 3.5 cm. in diameter. The steles are essentially radially symmetrical with a very slight tendency towards endocentricity.

It may be argued that some of the smaller vascular strands (fig. 14, S3 and S8) do not constitute true steles. However, even the smallest possesses 8 or more layers of secondary wood and can be seen to be independent in its course throughout the entire length of the specimen (fig. 13). Neither can they be designated as accessory strands from which leaf traces might be produced (as in *Sutcliffia* and M. *anglica*) since the two largest of the 8 steles are, in our specimens, the sole observed source of trace departure.

The primary wood is small in amount and is characterized by the almost complete absence of parenchyma; what little there is being restricted to a thin network running through or enclosing the primary cylinder, from which the high uniseriate rays extend out through the secondary wood. The primary wood forms a cylindrical to irregularly shaped core around which it is often difficult to determine the exact inner limits of secondary growth. The protoxylem is not distinguishable (figs. 14 and 19).

The secondary wood is variable as to cell size and radial growth, the first-formed layers being often composed of large tracheids (similar in size to the metaxylem) which merge some distance out into rows of much smaller cells. On

---

[1]The interpretation as to lower and upper surfaces of the stem is made on the basis of the outward passage of leaf traces exposed in a series of longitudinal peels.

the other hand, the same stele may, on the opposite side, show the first-formed secondary wood to consist of very small (in diameter) tracheids and the successive outermost cells to be large (fig. 19).

Each stele is enclosed by a dark tissue of crushed cells, probably of cambium and phloem, in which are occasional small resin canals. The entire stelar assembly is surrounded by a very thin, parenchymatous "periderm" which is never over 2 to 3 cells thick and is often so poorly preserved as to be indistinguishable from the cortex.

The rays are up to 1 cm. or more in height and apparently constantly uniseriate. In this regard they probably come closest to Andrews' (1940) classification II B in which he originally placed all of the Anglorota group as well as M. Noei and M. Leuckarti.

The cortex is composed of cells rounded in transverse view but elongated vertically two to three times their width. Traversing upward and outward through the cortex are numerous small collateral leaf traces consisting solely of 3–4 proto-xylem tracheids with spiral thickening (fig. 27) and an abaxial phloem group. There is definitely no secondary wood associated with the trace. Mucilage canals with their "resin rodlets" are scattered sparingly through the cortex and are un-usually small, having a constant diameter of less than 60 μ. They are commonly closely associated with the leaf traces and, in contrast to the majority of the other American species, seem to have seldom invaded the hypodermal, sclerotic strand zone.

The sclerotic strands form a single layer and in transverse view appear circular to slightly radially elongated. They are separated by 2–3 layers of cortical-like cells from a conspicuously darkened epidermis. This latter tissue consists of brick-shaped cells with a slight tangental elongation and rather thick walls which oc-casionally show evidences of a cuticle.

Discussion:

Our specimen shows a rather close similarity to Medullosa Thompsonii in the secretory canals—their small size, their comparative scarcity in the stem as a whole, and their almost complete absence in the sclerotic fibrous zone. However, although Andrews (1945) points out that the number of steles in the Medullosae is generally an unreliable taxonomic character (stelar divisions and fusions often resulting in variations of 2–3 or more steles), the possession by Medullosa primaeva of 7 to 8 steles, which tend to pursue horizontal courses through the stem and almost com-pletely lack conjunctive primary parenchyma, clearly makes it of specific im-portance and distinct from M. Thompsonii.

Medullosa centrofilis and M. pusilla are the only other species which seem similar enough to deserve consideration. The former comes closest to M. primaeva in number of steles (considering the "star ring" as a fourth stele) but lacks the hori-zontal stelar meanderings and exhibits many more and larger secretory canals. M.

pusilla is comparable in over-all stem size but again is separated by the stele number, the difference between 3 and 7–8 being held as more than specific variation.

The slight tendency toward endocentricity of the secondary wood and paucity of conjunctive parenchyma in the primary area, along with its generally netted arrangement, make the individual steles more closely comparable to those of *Microspermopteris* than to *Heterangium*. According to Bower's (1930) "size and form" principles one would expect relatively little parenchyma in steles of such small size, but comparison with the equally small stele of M. *Thompsonii* seems to show greater differences than can be accounted for on the basis of Bower's hypothesis. Thus although the M. *primaeva* stelar number is much larger than in any of the other species of equivalent age the general stele structure appears to be more primitive. This is in contrast to what might be considered advanced development as evidenced by the absence of secondary wood in the leaf traces and leads one to believe that the presence of such secondary wood in M. *anglica* is not necessarily indicative of a primitiveness either for the character or the species as a whole. On the contrary, it seems most logical at present to consider M. *primaeva* with its numerous small, radially symmetrical steles as having developed from a monostelic stem through stelar proliferation and accordingly representing a primitive stage of the genus.

The specific name *primaeva* has therefore been assigned.

Diagnosis:

Stem small, not exceeding 3 cm. Steles numerous, 6–8, frequently fusing and dividing, ranging from .5 to 5 mm. in diameter, often pursuing a sinuous horizontal course through the stem. Primary wood parenchyma small in amount or lacking. Resin canals small and few, almost entirely absent from fibrous hypodermal zone. Rays uniseriate; secondary wood of variable cell size; irregular radial growth, only slightly endocentric.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 14. Slide 1615 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Medullosa elongata, sp. nov.

The following description is also based on coal-ball material collected by Mr. F. O. Thompson and his associates of Des Moines, Iowa. The source was a large open pit mine of the Atlas Coal Co. located in Wilson County, Iowa. The horizon is Pennsylvanian, Des Moines Series.

The greater part of material from this locality was too heavily pyritized to permit good plant preservation, but the stem fragments which were identifiable indicate a flora consisting primarily of *Lepidodendron* and *Calamites*. Pteridosperms were relatively rare, the present description being based on a single stem specimen 7 cm. long and 6 x 1.5 cm. in diameter. There evidently had been some crushing, which would account partially, but not altogether, for the asymmetry (fig. 16).

The outstanding feature of the three steles is their extreme endocentricity in which character they resemble Schopf's (1939) *M. distelica*. The steles maintain their individuality, i.e., no stelar fusion, and relative position throughout the 7 cm. of stem length with the endocentric secondary development also showing a constant approximate 4 to 1 ratio in thickness as compared to the exocentric secondary tissues. The three steles are of equal size, averaging 10 $\times$ 2 mm., the plane of elongation following that of the stem as a whole and constituting a factor in the evidence that the general asymmetry was a natural character of the living plant. Two of the steles occupy a position directly opposite one another and near the center of the stem while the third is isolated off to one side (fig. 17). The primary xylem consists of a long narrow area following the elongation of the stele. It is seldom over 2 cells in width and runs up to 8 mm. in length. The metaxylem tracheids are large (.2 mm.), and usually triangular in cross-section. There is relatively little conjunctive parenchyma, while the protoxylem is indiscernible.

The secondary wood is rather unusual for a *Medullosa* in that the majority of the cells are square in transverse view, while the others are of the more characteristic alternately arranged pentagonal shape. Also, in contrast to the somewhat similar *M. distelica*, the radial rows of secondary tracheids are not conspicuously divided by rays nor are the outermost cells differentiated. In addition, the rays are uniseriate, not particularly numerous, and almost impossible to detect in transverse view.

Surrounding each stele is a thin dark layer of crushed cells containing numerous small resin canals. The periderm is thin (3–4 cells), poorly preserved, and apparently interrupted at the narrow ends of the steles where the leaf traces are given off. The cortex is rather poorly preserved due to pyritization, with numerous rather large slime canals (.2 mm. in diameter) scattered throughout it and also conspicuously associated with the fiber strands in the sclerotic-fiber hypodermal zone. The fiber strands are arranged in 2–3 alternating rows, the individual strands being somewhat radially elongated. A rather striking character of the species is the large "compound" resin canals running horizontally through the stem. They measure 1.3 mm. in diameter and are approximately six times the size of the vertical canals. Figure 18 illustrates several of these canals at the same magnification as the vertical canals in fig. 17. They are lined with numerous small triangular and diamond-shaped secretory cells which appear to contain the same black resin substance as the canal itself.

The leaf traces are given off from the narrow ends of the flattened steles and are initially quite large, consisting of 10–12 or more primary tracheids which divide farther out in the leaf bases into numerous smaller bundles. Three leaf bases are shown in fig. 16, two detaching themselves from the narrow transverse extremities of the stem and approximately parallel to it, while the third is being given off from the stem's broad side and at right angles to it. Thus it would appear that in *M. elongata* we are dealing with a creeping stem of possibly dorsi-

ventral symmetry. As stated earlier, the dimensions of 6 × 1.5 cm. for the stem can be only slightly attributable to crushing while the equivalent asymmetry of the steles and general lack of any crushed tissue indicate the form to be more or less characteristic of the living plant. In addition, the 7 cm. of stem length of our specimen exhibits rather short internodes, with several leaf bases given off in the same bilateral plane from the narrow opposite stem sides.

The position of the stem on the edge of the containing coal ball prevented observation of more than the one dorsal leaf base shown in fig. 16. However, it seems plausible that these erect leaves were produced between internodes as short as the lateral ones.

As implied previously, M. elongata is most closely comparable to M. distelica on the basis of the extreme endocentric secondary growth. However, in the possession of three steles, which at no time show any tendency towards fusion, the difference in primary wood, fewer and uniseriate rays, and square secondary tracheids, as well as the large compound resin canals and apparent dorsi-ventral habit, M. elongata is clearly distinct and of specific importance.

The species name elongata is assigned in recognition of the asymmetric transverse elongation of the steles (10 × 2 mm.), as well as the equivalent transverse elongation of the stem as a whole.

Diagnosis:

Stem asymmetric to bilaterally symmetric, approximately 6 × 1.5 cm. in diameter, only slightly crushed in the smaller dimensions. Steles 3, extremely endocentric, 2 opposite one another in stem center, the third isolated to one side, retaining their relative positions and not fusing or dividing in over 7 cm. of stem length. Vertical resin canals numerous, averaging .2 cm. in diameter; fewer horizontal, large compound resin canals averaging 1.3 cm. in diameter. Habit creeping or climbing with leaves being given off from sides and dorsal surface of stem.

Locality: Atlas strip mine, Wilson County, Iowa.

Horizon: Pennsylvanian, Des Moines Series.

Type Specimen: Fig. 16. Slide 1617, in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Medullosa endocentrica, sp. nov.:

This third new medullosan stem comes from coal-ball material found in a stream bed outcropping near Berryville, Illinois. The location is near to that from which Steidtmann (1937) described M. Noei, and the horizon is the same, being determined as the upper part of the McLeansboro group of the Pennsylvanian of Illinois. The coal ball containing the specimen was 15 cm. long by 8 cm. wide. The stem followed a straight course through almost the complete longer axis, being itself 12 cm. long and 1.2 × .7 cm. in diameter. These dimensions are of the stelar system only, the cortex and other external tissues having been lost. However, as can be seen by referring to fig. 20, the unique appearance of the steles seems

to justify recognizing the specimen as a new species and possible culmination of endocentric development, in spite of the lack of information as to the stem's external anatomy.

The stem consists of 3 steles, 2 of which are 5 × 5 mm. in diameter, the third, 2 × 1.5 mm. in diameter, situated on the side equidistant between them. Secondary growth is almost entirely endocentric, only one of the larger steles showing a very small amount of exocentric growth. These characters are constant for the entire 12 cm. of stem length as are also the relative stelar positions. Thus there can be little doubt that this extreme centripetal growth was a distinct feature of the living plant, and the evidence also suggests that the stelar system had achieved a degree of uniformity not found in any of the other Anglorota species.

The primary area of each stele is oval in transverse view, and measures 1.5 × 1 mm. in the 2 larger steles. It consists of scattered groups of large metaxylem cells intermixed with considerable conjunctive parenchyma. The protoxylem appears to consist of two small exarch groups of tracheids with annular thickening while the metaxylem shows the characteristic dense reticulate bordered pitting.

The secondary growth is produced in a fan-like pattern, radiating towards the stem center for an average of 15 cells in the large steles and 6 cells in the small stele. The transverse dimension of the cells increases gradually from the innermost to the outer rows but on the average is quite large, around .2 mm. The rays are of great height, more than 1.7 cm., and in the wood are uniseriate or at the most 2 cells wide. They commonly separate radial rows of 2–3 tracheids (fig. 22).

The pitting of the secondary wood is bordered and densely reticulate on the radial and oblique-tangential walls, with relatively few scattered pits on the directly tangential surfaces. The length of the individual tracheids is also quite extreme, an almost perfect tangential section showing them to be over 1.7 cm. Adjoining the outermost secondary wood (and continuous with it in general pattern and ray position) is a rather disorganized tissue which we were at first inclined to interpret as undifferentiated secondary wood. It consists of large thin-walled cells, similar in size and shape to the secondary tracheids but completely unpitted. On entering this zone the thin rays of the wood become greatly expanded, averaging from 4 to 8 or more cells in width, and appearing to be completely mature in their development (fig. 21). This point, along with the total absence of any rudimentary pitting, in either the tangential or radial walls of the vertical elements, in our opinion, makes it very unlikely that the cells are immature secondary tracheids. On the other hand, one or two of our tangential peels through this zone shows vestiges of what appear to be disarranged transverse walls with extremely small pores similar to the sieve plates of living plants (fig. 23). Scott, in his description of M. anglica, has pointed out that the rays become much wider in the phloem zone, while exceptionally large sieve tubes are common to plants of vine-like habit. Therefore, on the basis of the above evidence (which may be not entirely conclusive), along with the position of the tissue, we are inclined to consider it tentatively as phloem-like in nature.

Lying between this phloem region of the three steles is a thin parenchymatous zone of vertically elongated cells in which are scattered numerous resin canals containing their opaque resin rodlets. The entire stelar assembly is completely surrounded by a thin layer of dark, crushed cells of possible periderm nature.

The specific name *endocentrica* is assigned on the basis of the complete and constant centripetal secondary growth.

Diagnosis:

Steles small, not exceeding 5 × 5 mm., 2 opposite one another and of equal size, the third smaller, situated on the side between them. Secondary growth completely centripetal. Primary xylem exarch. Metaxylem with considerable conjunctive parenchyma. Rays 1–2 cells wide, expanding in the conspicuous phloem zone to 4–8 cells in width, exceeding 1.5 cm. in height.

Horizon: Upper part of the McLeansboro group, Pennsylvanian of Illinois.

Type: Fig. 20. Slide 1619 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Discussion:

As stated previously, *Medullosa endocentrica* appears to represent the ultimate in centripetal secondary development, and accordingly its closest affinities lie in the direction of *M. distelica* and *M. elongata*. It differs from the former primarily in possessing a third distinct small stele, constant for the whole stem and in the more perfect symmetry of the opposing "twin" steles. It differs from *M. elongata* in stele shape (*M. elongata* averaging 10 × 2 mm.), as well as in the character of the primary wood and amount of conjunctive parenchyma. *M. endocentrica* differs from all the other Medullosas in its constant degree of endocentricity and the possession of a unique phloem zone of exceptionally large sieve tubes.

It is possibly significant that here, as in *M. elongata*, we appear to be dealing with a stem of more bilateral (dorsi-ventral) than radial symmetry. From the form of stele development in *M. endocentrica* (fig. 20) leaf traces could only have been given off in the three planes opposite the abaxial sides of the primary xylem groups. Thus while the orientation of the steles is somewhat different in the two species it is likely that the phyllotaxy was similar, the leaves being produced laterally and vertically (dorsally) with the side lacking a leaf trace source being considered ventral.[1] The predominance of 3 stele forms in the Medullosae is perhaps indicative of this trend, which, however, reaches its inescapable climax only in the extremely endocentric species. *M. endocentrica* has apparently almost reached the limit of its potential stem enlargement through secondary growth but it is still much too small to permit interpretation is an arborescent plant. Therefore it could not possibly

---

[1] It should be pointed out here that since the traces show no evidence of "girdling," the direction of their initial departure is a valid indication of the stem's phyllotaxy.

have attained a habit comparable to that suggested in the reconstruction of M. *Thompsonii* (Andrews, 1945). Also if it produced relatively large *Alethopteris*-type fronds, as appears likely from the numerous associated leaves, it must have been a prostrate or climbing vine since the small stem would be incapable of supporting any such great weight. Thus the line of endocentric development from *M. distelica* and *M. elongata* to *M. endocentrica* appears to be one leading to constantly diminishing size accompanied by a change from radial symmetry of the stem with complete spiral phyllotaxy to a bilateral, dorsiventral symmetry with lateral and dorsal leaves. Extreme asymmetry can accordingly be seen to be an advanced rather than primitive character, which as it reached its climax resulted in a line of "dead-end" development in which the stem size was small and fixed. In this viewpoint we agree with Schopf (1939, page 204) where he states:

> It seems more tenable to consider the distelar condition in the new Nashville *Medullosa* as reduced from a more polystelar type rather than as directly derived from an ancestry reminiscent of *Sutcliffia*. It is also apparent that the extreme endocentric asymmetry found in *M. distelica* is not a primitive feature.

We have included in the above quotation Dr. Schopf's statement on a distelar condition probably resulting from the fusion of a polystelar type in that it also agrees with our conception of what seems to be another and more important line of development in the Medullosas. As pointed out in the discussion of *M. primaeva*, a polystelar condition with numerous small radially symmetrical steles would seem to have arisen most logically by stelar proliferation of a monostelic stem with a similar small symmetrical stele. Then through subsequent tendencies to stelar fusion the line would lead through the small tetra- and tri-stelar forms to the large asymmetric stelar forms such as *M. anglica* and *M. Noei*.

The fact that the smallest species (*M. primaeva* and *M. pusilla*) have the most radially symmetrical steles while the larger species (*M. Thompsonii*, *M. elongata*, *M. distelica* and *M. anglica*) all have greatly elongated (transversely) asymmetric steles is evidence, in our opinion, that the latter have been derived from polystelic fusion. (A good example of this point is illustrated in Andrews' (1945) diagrams of stelar fusion in *M. Thompsonii* where it can be seen that the fusion produces a larger, more asymmetric and more endocentric stele). Where the fusion standardized itself at 3 steles of approximately equal size, or with one slightly smaller, a balance appears to have been reached which was only upset by the origin of the erratic cambial growths of *M. Noei*.

Regarding the phyllotaxy of the predominately 3-steled forms it may also be pointed out that while the leaf arrangement has been mainly interpreted as spiral, Scott, in working with a specimen of *M. anglica* one foot in length, showed that the leaves were still produced on only three sides of the stem (text-fig. 1). While Scott himself did not enlarge on this evidence, it seems to imply (when correlated with forms such as *M. elongata* and *M. endocentrica*) that the significance of the normal number of 3 steles in the Carboniferous Medullosas lies in the essentially

dorsi-ventral habit of the plant as a whole. As may be noted in text-fig. 1 of M. *anglica* (which is typical for most of the 3-stele species), the steles are arranged in the shape of a flattened triangle, the obtuse apex being always towards the flattened side of the stem from which the dorsal leaf bases are produced, while the steles at the opposite acute angles are oriented towards the position of the lateral leaves.
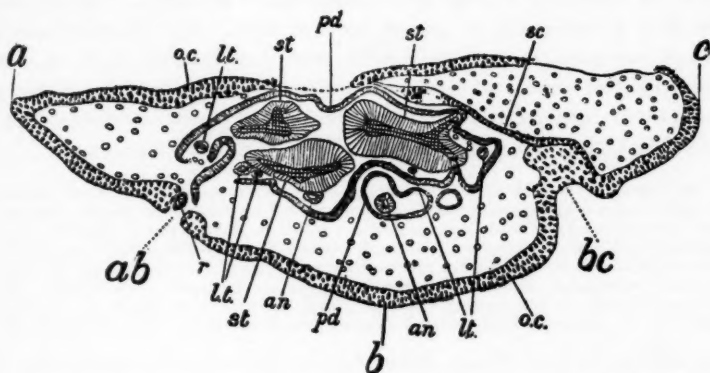
Text-fig. 1. *Medullosa anglica:* *o.c.*, outer cortex; *l.t.*, leaf trace; *st*, stele; *pd*, periderm; *sc*, sclerotic strands separating petiole from stem; *r*, root; *an*, accessory strand. *A, B, C, AB* and *BC* represent the points of leaf departure with the phyllotaxy being 2/5. *Note that this arrangement still leaves one side of the stem completely devoid of leaves; so that the habit may be assumed to have been dorsi-ventral* (after Scott).

This bilateral symmetry is borne out also in the over-all stem shape of nearly all of the 3- to 4-steled group. *M. centrofilis* had a stem diameter of 5 × 1.5 cm.; *M. pusilla*, 2.2 × 1.3 cm. (Scott points out that the larger diameter here had lost considerable tissue and was probably still greater in life); *M. Thompsonii*, 7 × 2.5 cm.; *M. anglica*, 10.5 × 3.7 cm.; *M. elongata*, 6 × 1.5 cm. *M. endocentrica* also undoubtedly had a flattened stem but the lack of preservation of the outer tissues in our specimen precludes such measurements. All of the above figures include the attached leaf bases, but since it has been shown that these were always decurrent for long distances on the stem and more or less overlapped, the measurements give a truer habit proportion than those of the stem alone would. The asymmetry can be seen to be quite constant in a proportion of 3:1, which fact alone makes it extremely doubtful that it is altogether due to crushing. De Fraine states for *M. centrofilis* that "the shape of the stem with its covering of leaf bases was thus distinctly flattened."

It would seem that the dorsi-ventral habit, while most obvious in species such as *M. elongata* and *M. endocentrica* was also the rule in the majority of the other species. *M. Thompsonii* is a possible exception since rather careful study of the type specimen seems to indicate that in this particular stem the orientation of the stelar assembly tends to vary, so that the planes of leaf trace departure are dis-

tributed more generally in the four opposing radii and thus supply petioles in a true radially symmetrical spiral phyllotaxy. However, such variations are not too unusual. *Selaginella,* for example, in the two present-day species, S. *rupestris* and S. *apoda,* shows a variation from erect plants with radial symmetry to creeping plants with bilateral symmetry. This view, accordingly, makes it necessary to visualize the Medullosae as primarily an assemblage of creeping or climbing plants rather than as comparable to present-day tree ferns. The prostrate habit has previously been postulated by several earlier workers on the basis of the small stem of the Anglorota plants, while the great stem length recorded by Weber and Sterzel (1896) for some of the Permian specimens is almost conclusive proof of the vine-like habit of the much younger species. Weber and Sterzel state:

> Bei Stämmchen wie M 43, das bei 92 cm. Länge nur einen Durchmesser von durch-schnittlich 8,8:4.4 cm. besitzt, könnte man wohl an die von Göppert & Stenzel vermutete Schlingpflanzennatur der Medullosen denken. . . . Die im Anhang sub 1 Seite 105 (64) geschilderten Medullosenstämmchen beweisen dass insbesondere *Medullosa stellata* eine schlank-cylindrische Gestalt mit periodischen Anschwellungen des Holzkörpers und auch im Uebrigen merklich wechselndem Durchmesser haben könnte, so das man, wie schon erwähnt, mit Göppert & Stenzel an Schlingpflanzen denken könnte. In dieser Form des Wachstums liegt wohl auch das verhaltnismässig häufige Vorkommen von Bruchstücken dieser Art begründet.

In addition to the evidence offered by the dorsi-ventral flattened stem, the phyllotaxy, and the great stem length in relation to its width, there is also consider-able anatomical proof that the Medullosae were primarily prostrate or climbing vines. Solereder (1908) has shown that unequal xylem growth and flattened stems are characteristic of many living lianas, while Westermaier and Ambronn (1881) have pointed out that tracheids and sieve tubes of more than average diameter are typical of living climbing plants. As noted by Andrews (1940), the tracheids of M. *Noei* and M. *anglica* may reach a diameter of 250 μ (larger than most vessels) while M. *endocentrica* has extremely broad sieve tubes.

Although the acquisition of concentric rings of exocentric secondary wood permitted an increase in size of the Permian Medullosas, along with a possible return to a radially symmetrical spiral phyllotaxy, the vine-like habit of their Carbo-niferous predecessors appears to have been largely retained.

The absence of a vine-like habit in the living or fossil cycads need not present any insurmountable difficulties in retaining the theories of their origin from the Medullosas, since, with the increased girth afforded by centrifugal secondary growth, the developmental trend may be assumed to have been away from climbing towards arborescent forms. This change may also have been influenced and accompanied by a disappearance from the scene of the potentially supporting *Psaronius, Cala-mites* and *Lepidodendron* through a gradual shift to a xerophytic environment.

To summarize and restate our evidence:

1.   A large number of small symmetrical steles with almost solid primary wood represents the primitive condition. Of the different specimens which have so far
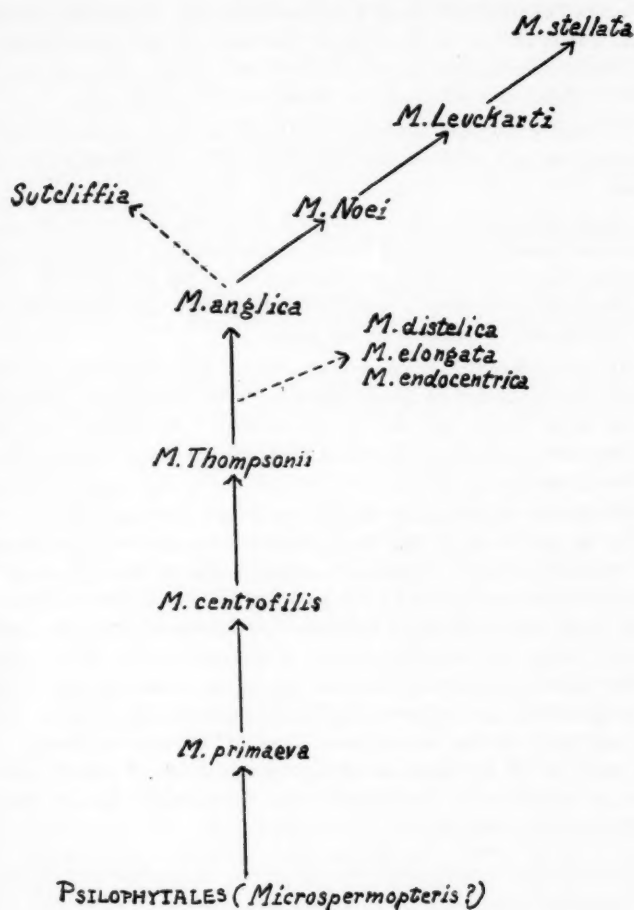
Text-fig. 2.   Proposed *Medullosa* phyletic chart.   Explanation in text.

been described, M. *primaeva* seems to most nearly represent this stage.   In this light it seems probable that the origin was not from *Heterangium* but rather from a more ancient form possibly akin to *Microspermopteris*.   Arnold (1940) has described a small polystelic stem from the Middle Devonian of New York to which he has given the name *Xenocladia medullosina*.   It consists of 9–10 small (not much over 1 mm.) steles with a small solid protostele.   He states that: "*Xenocladia* may eventually prove to be a representative of some intermediate stage between the Psilophytales and certain of the polystelic Pteridosperms."   While we

are not inclined to attach too much weight to any direct connection between *Xeno-cladia* and a stem such as M. *primaeva,* it does show the possible origin of a poly-stelic structure contemporaneous with *Rhynia* and *Hornea* and, along with *Micro-spermopteris,* indicates a psilophytalian origin for the pteridosperms.

2.   Through subsequent tendencies to fusion the stele number eventually be-came standardized at 3, with occasional variations of 2 or 4 through further fusion or division.

3.   Accompanying the above transition there was an increase in the size of the plants and consequently of the leaves, which (since in a closely grouped poly-stele the leaf traces of necessity are produced from the abaxial sides) tended to inhibit exocentric (centrifugal) secondary growth and thus resulted in an endo-centric (centripetal) asymmetry of the steles.

4.   As this endocentricity became pronounced the production of leaf traces also became more localized on the abaxial stelar sides, resulting in a phyllotaxy of lateral and dorsal leaves (text-fig. 1, M. *anglica*).   M. *elongata* and M. *endo-centrica* represent a climax of this trend which in the latter undoubtedly formed an end development.

5.   Where the endocentricity did not reach such extremes, the plants tended to increase in size through the production of accessory vascular strands *(M. anglica),* while eventually tangential secondary growth (to compensate for the limitations of endocentric growth), along with the origin of prolific erratic cambial zones *(M. Noei),* led to the larger and more complex Permian species.   Text-fig. 2 shows a provisional and tentative phyletic chart based on the above points.   Al-though the horizon of all of the American species is considerably higher than that of the European ones, the evidence of the stems themselves still seems to justify the reverse grouping.   For the reasons given above M. *primaeva* constitutes the base with the main line of development leading through M. *Noei* and M. *Leuckarti* to the Permian forms, while the three extremely endocentric species constitute a dead-end side chain of development.

Medullosa anglica is placed near the top because of its relatively large size and erratic "periderm" resembling that of M. *Noei*.   The large leaf traces with sec-ondary growth may be viewed as advanced and of the nature of specialized ac-cessory vascular strands to supply the increased needs of the enlarged petioles.   Also *Sutcliffia,* differing from M. *anglica* primarily only in its monostelic structure, may be regarded as resulting from a fusion of the three steles.

Medullosa Noei Steidtmann:

Steidtmann (1937, 1944) established M. *Noei* as the first clearly recognizable American species of the genus and gave us an excellent description of the salient features and peculiarities of the stem as well as the associated leaves, roots, and seeds.   However, the holotype on which he based most of his description had only

one stele with portions of two others, while our present specimen consists of a nearly entire stem with three large complete steles. It was collected from the same outcrop near Berryville, Illinois, that produced M. *endocentrica* and is exceptionally well preserved in its cellular details. The coal ball, of which the stem constituted almost the entire bulk, was 28.6 cm. long and approximately 16 × 7 cm. wide in the middle portion, tapering to blunt points at either end.

The essential features offering possibilities of an enlarged interpretation and understanding of the species are:

1. The presence of a distinctive phloem zone characterized by broadened extensions of the medullary rays.

2. "Periderm rings" which show a transitional development of secondary wood, a stelar origin, and a remarkable similarity to the Permian Medullosae "star-rings."

3. Adventious roots, which run for long distances through the cortex parallel to the steles, range from triarch to pentarch, and show a well-preserved aerenchymatous cortex.

Before discussing these points in detail a brief description of the stem as a whole will be given. As shown in text-fig. 3, there are three large steles, tangentially elongated, which occupy the major portion of the area as seen in transverse section. Throughout the 28.6 cm. of stem length they remain essentially independent although steles *a* and *c* occasionally partially fuse and then re-separate. Their orientation with relation to one another is similar to that of the steles in M. *elongata,* two of the steles being side by side while the third occupies a position off to one side. They average 6 × 1.5 cm. in diameter and show no particular endocentricity, the secondary growth being the greatest in a tangential plane rather than towards the stem center. This is a greater elongation than was usual in Steidtmann's specimen, although he records that the stele did at times reach a measurement of 6 × 1.8 cm., which is certainly close to the above. For the rest, the primary and secondary wood are essentially equivalent to Steidtmann's specimen and exhibit primary tracheal bundles, prolific and erratic "periderm" growths, and tetrarch roots originating in and running through the primary area. The cortex is crowded with "periderm" rings and tangentially elongated bands, as well as with the numerous large adventitious roots with their many small branches. The hypodermal sclerotic zone is present as the outermost limiting tissue, the leaf bases being absent. While there are apparent general differences between the present specimen and Steidtmann's diagnosis of M. *Noei* (mainly in the lack of any pronounced endocentric growth, and absence of a definite broad periderm zone), it is felt that the variations fall within those allowable to a species, particularly in the Medullosas. The following descriptions of the previously outlined characters are therefore intended solely as an addition to the M. *Noei* diagnosis and not as of new specific or varietal importance.
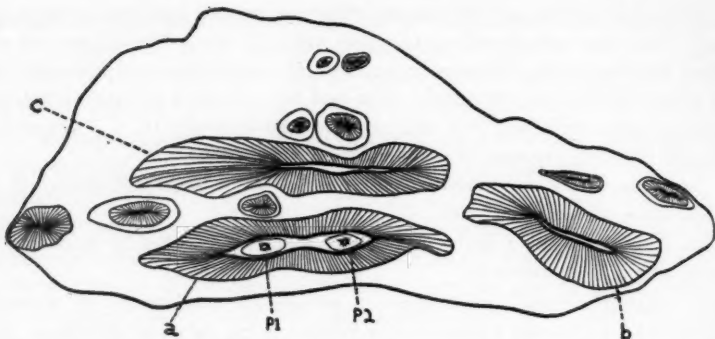
Text-fig. 3. *Medullosa Noei: a, b,* and *c* indicate the three steles. *P1* and *P2* are the "periderm" or "cambial" rings. All of the other vascular strands represent adventitious cortical roots. Additional explanation in the text. $\times$ 4/5.

It is understandable how a great deal of the M. *Noei* material might be examined without observing the striking phloem rays, since they are only occasionally evident even in the exceptionally well-preserved present specimen, their place being usually occupied by invasions of the prolific "periderm" tissue. However, as shown in fig. 26 the rays with their dark brown secretory cells sometimes form a quite prominent fringe around the stele. They vary from 1 to 2 mm. in length (outside the wood) and from 4 to 8 cells in width, spreading out fan-like towards their outer margin. The cells are radially elongated and contain numerous black globules of evident secretory nature. The tissue lying between the rays is seldom well preserved. Whatever sieve tubes that might have once existed are consistently represented by disorganized cellular fragments. The general aspect as seen in transverse section is rather similar to the expanded "phloem rays" of M. *endocentrica,* the rays in both species being characterized by their dark brown color and black secretory cells, as well as in their greater width as compared to their structure in the xylem.

As mentioned previously, numerous adventitious roots run through the cortex. They vary from tetrarch ones, which apparently originate in and run through the primary part of the stele for some distance before emerging, to triarch and pentarch ones, which seem to arise in the "periderm" adjoining the stele and follow a vertical course through the cortex for long distances before emerging. Some of these cortical roots attain considerable size (up to 2 $\times$ 2.5 cm.) and are sometimes difficult to distinguish from small steles (text-fig. 3). They are often beautifully preserved and show an aerenchymatous cortex, a feature strongly suggestive of a moist or aquatic habitat (fig. 25).

It may be pointed out here that Worsdell (1906) has found that the Cycadaceae show a similar variability in root anatomy with pentarch or tetrarch roots normally borne adventitiously near the base of the plant and the diarch and triarch roots produced towards the apex.

In Steidtmann's (1937) preliminary report he stated that M. *Noei* apparently had three large steles with at least two "star rings." Later, in his more intensive and complete treatment of the species (1944), he indicated that the structures which he had initially reported as "star rings" proved on closer observation to be "large concentric strands of the ever-present periderm." Now, our present specimen seems to show that Steidtmann's first view was the correct one and that the periderm or "cambial" rings possibly do represent developing "star rings."

De Fraine (1914) points out that the "star ring" of M. *centrofilis* differed from the star rings of the Permian stems in that it was basically protostelic while the latter, as implied by the constant reference to a "partialmark," were largely parenchymatous. This distinction is shown in pl. 10, where not only the difference between the M. *centrofilis* type of "star ring" and that of M. *stellata* is evident but also the considerable similarity between the latter and an M. *Noei* "cambial ring." Accordingly, the use of the term "star ring" for the fourth small stele in M. *centrofilis* was probably ill-advised, as it obviously had little in common with the majority of the structures so named in the Permian species but merely constituted a small independent stele. On the other hand, the evidence seems clear that in M. *Noei* we have, for the first time in a Carboniferous stem, the appearance of structures equivalent to the Permian "star rings." The fact that it was not until after a careful examination of his specimen that Steidtmann decided the structures were too similar to the profuse erratic periderm growths to be called "star rings" suggests that the "sternringen" of the poorly preserved, silicified stems of "des Rotliegenden von Chemnitz-Hilbersdorf" may also have been "periderm growths." Certainly the observable detail of the Weber & Sterzel specimens was hardly comparable to that to be found in good coal-ball material.

Steidtmann (1944) discussed the advisability of using the term "periderm" for these prolific growths, and came to the conclusion that it was valid since it did not necessarily imply suberization. However, in our specimen it can be seen that the tissue (at least that which forms many of the rings) originates in the primary part of the stele, and, instead of being an invasion from the cortex, itself produces outgrowths which occasionally penetrate the secondary wood and extrude into and through the cortex. Figure 24 shows a ring from the primary area of stele *a* (text-fig. 3) in which a certain amount of differentiation into secondary xylem has taken place, indicating that the tissue was more of a true cambial nature than periderm. That these "cambial rings," like some of the roots, originated within the stele is clearly shown by their continuous vertical course throughout the stele both above and below the occasional cortical invasions.

There is also the new evidence which has come to light in M. *Thompsonii* that the "star rings" may, in part, be derived from a *congestion* of leaf traces. Figure 59 shows a diagram of a portion of M. *Thompsonii* which has just given off a petiole. The hypodermal fiber strands are lacking on the one side and the cortical area containing the outgoing traces is considerably diminished. Arranged in a line along the stem margin in this area are numerous thin-walled xylem "rings" with a central core and radial secondary tissues (figs. 30 and 59). Successive peels, downward through the stem, show that these "rings" result from a fusion of two or more outgoing traces. It seems that the traces, while still being prolifically formed, lacked an expanding cortical area in which to scatter out, and consequently became congested and fused with a subsequent production of secondary growth. The limitations of the M. *Thompsonii* material do not allow observation of the final disposition of these "rings," but it seems likely, with the increase in the cortical area on approaching the next node, that the "rings" or "aggregate" traces may have redivided and lost their secondary wood.

If in the early ontogeny of the Permian Medullosas there were numerous leaf traces produced towards the center of the stem, the same congestion and fusion might possibly have resulted in the medullary "star rings" of M. *Solmsii*, with the central position inhibiting subsequent redivision. We are inclined to follow Worsdell (1906) rather than De Fraine (1912) in that (as pointed out in the previous discussion) we regard the Permian Medullosas as leading to the Cycads, with *Sutcliffia* as an advanced rather than primitive member of the Medullosae. The above theory of a leaf trace origin for the "star rings" would offer further evidence for Worsdell's view that the collateral rings of the Permian Medullosas and the Cycads are "composed of the one-sided remnants of a number of steles," since only in such a polystelar structure could the leaf traces be produced towards the center.

To pursue the conception still further, De Fraine (1912) states: "There appears to be no serious objection to the view that the 'meristeles' of *Sutcliffia* are homologous with the leaf trace strands which leave the stele in M. *anglica* for both appear to be entirely used up in the formation of foliar bundles." Following the same reasoning, the marginal vascular rings in M. *Thompsonii* may also be considered as homologous to the above in that they differ only in forming in the cortex rather than at the stele margin, while the Permian "star rings" may also be homologous except that they were not used up in the formation of foliar bundles due to their internal position. Thus the extra-fascicular zones and accessory cortical and pith strands (star rings) of *Medullosa, Sutcliffia,* and the present-day Cycads are possibly all equivalent in that they may represent aggregations of fused leaf traces around which the secondary growth has become concentric producing rings or (where adjoining groups become contiguous) forming collateral bands.

SOME MICROSPORANGIATE FRUCTIFICATIONS ASSIGNED TO THE MEDULLOSAE

The abundance and variety of *Medullosa* stem and petiole remains in the Iowa and Illinois coal balls indicate clearly that the group was a dominant and wide-spread feature of the Carboniferous flora. As Andrews (1948) points out: "The wide range in anatomy exhibited by the Upper Carboniferous and Permian medullosas almost certainly represents an assemblage of familial or possibly ordinal rank rather than simply a genus." Accordingly, it is not surprising to find a corresponding diversity beginning to be evidenced among the other organ genera usually associated with and regarded as belonging to the *Medullosa* stems. This is particularly true of the interesting microsporangiate fructification known as *Dolerotheca*. *Dolerotheca* is characterized by a large campanulum containing radially arranged rows of paired tubular sporangia. The evidence for its being a medullosan pollen-bearing organ is almost conclusive although it has not as yet been found attached. Dr. J. M. Schopf (1948), in addition to describing three new species from Illinois coal balls, has given a comprehensive historical, taxonomic, and phylogenetic discussion of the genus and certain allied forms. Therefore we shall limit ourselves here to describing briefly two additional new species of *Dolerotheca* from coal-ball material collected at the What Cheer Clay Products Co. coal mine, What Cheer, Iowa. This horizon is designated only as the Des Moines Series, Pennsylvanian, but as we shall point out later may be tentatively assumed to be of considerably greater age than the lowest Illinois horizon in which petrifactions of *Dolerotheca* have been found.

Dolerotheca sclerotica, sp. nov.:

The general shape is that of a broad rather shallow campanulum approximately 25 mm. in diameter and 5–7 mm. deep (fig. 45). The epidermis of the proximal sides is represented by a layer of tangentially elongated cells with conspicuous dark contents, on which are scattered a few very small capitate glandular hairs (fig. 58). Just within this layer is a definite sclerotic hypodermal zone, .4 mm. in thickness, of empty isodiametric cells, only approximately 1 out of 30 showing a black secretory plug (fig. 49). Lying immediately inside this latter zone is the parenchymatous ground tissue of the fructification which, as in the Illinois species, seems to enclose and "constitute the walls of the sporangia." It forms a network of uniform thickness, 2–3 cells, composed of thin collapsed parenchyma in which are numerous large secretory canals with their dark, opaque contents.

The double radial rows of tubular sporangia are separated by very conspicuous sclerotic bands, 4–6 cells thick, which are normally interrupted at the junction with the alternating lysigenous tubes but may occasionally form almost continuous radial septa from the center of the fructification out to the marginal ground tissue. The individual sclerotic fibers are small, 50 μ in diameter and up to 500 μ in length. The bands bifurcate from 1 to 3 times, the first time about $\frac{1}{4}$ the distance from the center, the second at about half the distance from the center,
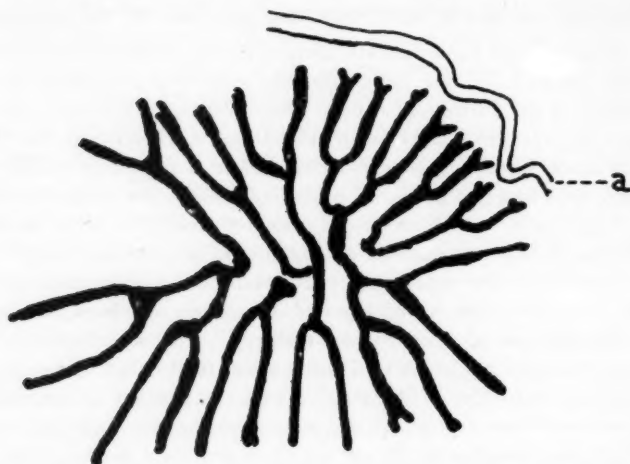
Text-fig. 4. *Dolerotheca sclerotica:* Diagram showing pattern of bifurcations of sclerotic-fibrous framework. *a*, campanulum wall. Explanation in the text. × 4.

and the third time within 1 mm. or less of the marginal peripheral ground tissue (text-fig. 4). Additional paired rows of sporangia are intercalated at the inner bifurcations while the marginal division is generally too near the periphery to allow space for more than the insertion of a single sporangium. The lysigenous tubes are much less conspicuous than in the three Illinois species. In the latter the tubes are enclosed by walls 3–6 cells thick, having circular to oval locules, while the equivalent structures in *D. sclerotica* are represented merely by rectangular spaces between the thin (1 cell) tangential walls of adjoining sporangia (figs. 48 and 50). As in *D. formosa* Schopf, the vascular bundles of our specimen "are noteworthy for their obscurity." They consist of 3–4 small annular tracheids apparently restricted to the marginal area of the campanulum. The bundles lie in the secretory parenchymatous tissue which alternates radially with the sclerotic bands, there usually being but one bundle in each radial strand 1 mm. within the hypodermal zone.

   D. sclerotica appears to have had considerably less dehiscence tissue than the Illinois species, although the distinction is possibly doubtful since our specimen was poorly preserved at the distal end. However, as shown in fig. 48, the groundwork of the fructification consists solely of the fibrous sclerenchyma bands with a parenchymatous network of secretory cells, and it is only at the extreme periphery that fragments of tissue of possible dehiscent nature are found. The sporangia average 500 × 700 μ in diameter, only the centermost being vertical. The outer sporangia originate on the ascending inner slope of the campanulum and tend to

follow the general shape, curving outward and upward (fig. 45). The spores are unusually large averaging 470 × 200 μ, in the longer dimension exceeding that of all of the Illinois species. They are marked by a monolete suture similar to that described for *D. formosa*.

The major distinctions between *D. sclerotica* and the three Illinois species—*D. villosa, D. Reedana* and *D. formosa*—are as follows:

1. Few very small capitate epidermal hairs as compared to the relatively dense pubescence of the other three species.

2. A homogeneous sclerotic hypodermal zone.

3. Lysigenous tubes which are merely gaps between thin-walled sporangia.

4. A dominating radiating framework of bifurcating fibrous sclerenchyma bands.

5. A greater amount of secretory cells in the parenchymatous ground tissue.

6. Larger prepollen or spores.

The differences may be said to be almost of generic importance and scope and lend further weight to the viewpoint voiced earlier that the Medullosae are probably a more heterogeneous group than can much longer be contained in a single genus.

Diagnosis:

A flattened campanulum up to 25 mm. in diameter. Epidermis of dark secretory cells, practically glabrous, with only a few capitate hairs. A conspicuous hypodermal zone of isodiametric sclerenchyma cells. Groundwork composed of radiating, bifurcating bands of fibrous-sclerenchyma enclosing a parenchymatous secretory tissue which composes the sporangial walls. Lysigenous tubes consisting solely of gaps between thin tangential sporangial walls.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 45. Slide 1628, in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Dolerotheca Schopfii, sp. nov.:

This species, like *D. sclerotica*, is based on a single specimen also from the What Cheer coal mine near the town of What Cheer, Iowa. The fructification had evidently been broken into fragments prior to fossilization since, although cellular preservation is excellent, only an estimated one fourth or less of the campanulum was present in the coal ball. However, from the individual sporangia (up to .6 × 1.3 mm. in diameter and their incomplete length of 15 mm.) it is possible to assume that the complete structure was comparable in size to *D. formosa* and possibly more tubular due to its apparent greater depth (figs. 51 and 53). Thus, it is considerably larger than *D. sclerotica*. Unlike the latter species also, its proximal surface is covered with an extremely dense pubescence of glandular hairs up to 5–6 cells in length. The cells are flattened, 3–4 times as broad as long, the terminal cell being slightly tapered. All the cells contain black opaque secretory masses

(fig. 57). In the solid density of the hairs *D. Schopfii* is comparable to *D. villosa* but the gross appearance is closer to *D. formosa*.

Immediately within the hirsute epidermis is a broad (up to 1.5 mm. thick) hypodermal zone of large secretory canals (200 μ in diameter) scattered profusely throughout a homogeneous matrix of small fibrous sclerenchyma cells which average 50 μ in diameter to 500 μ in length. This zone is identical to and continuous with the ground tissue making up the tangential and central radial walls of the paired sporangia (figs. 46 and 47). The radiating framework of fibrous, sclerotic bands is not quite as prominent as in *D. sclerotica* but is still much more extensive than in any of Schopf's Illinois species. As in *D. sclerotica*, the radial bands are occasionally continuous for a space of 2–3 sporangia, although the more usual condition seems for the bands to have been interrupted at the point where they join the sporangial tangential walls (fig. 51). The individual fibers are approximately equal in size to those of *D. sclerotica*.

Probably the most distinctive character of the species is the apparent lack of lysigenous tubes which in the other species alternate radially with the tubular sporangia. While the fragmentary condition of the type specimen shows only a marginal portion of the original campanulum to a depth of about 6 sporangia, it can be clearly seen that the radially adjoining sporangia are separated only by a common wall of the secretory and sclerotic ground tissue (figs. 46 and 51). It is, of course, possible that this could represent an immature stage in which the cellular disintegration forming the lysigenous tubes had not yet taken place. However, the size of the fructification, which must represent considerable maturity, along with the apparent complete dehiscence of the spores, makes it seem much more likely that the lysigenous tubes were simply not developed in this species.

The vascular bundles are even more obscure than in *D. sclerotica*. They consist of only 1–2 annular tracheids and occupy a similar marginal position in the radial ground tissue just within the broad hypodermal zone.

As in *D. sclerotica*, there is no observable dehiscence tissue, which again may possibly be due to lack of sections through the distal end. Dehiscence had evidently been complete, and no spores were found in any of the sporangia.

In comparison with *D. sclerotica* and the three Illinois species the following characters of *D. Schopfii* are held to be of specific importance.

1. Absence of lysigenous tubes.

2. The broad secretory and sclerotic hypodermal zone continuous with and identical to the groundwork making up the sporangial walls.

3. The more tubular shape of the campanulum.

While the nearly glabrous stony outer tissues of *D. sclerotica* contrast strongly with the dense glandular hairs and thick secretory zone of *D. Schopfii*, the thick radial sclerotic framework in both, along with inconspicuous lysigenous tubes in *D. sclerotica* and complete lack of them in *D. Schopfii*, seems to show that the two species are much more closely related to each other than to the Illinois species.

The species is named in honor of Dr. James M. Schopf in recognition of his noteworthy work on the genus.

Diagnosis:

Campanulum an estimated 35 mm. in diameter and 15 mm. or more in depth. Proximal epidermis with a dense pubescence of broad glandular hairs; a broad hypodermal zone of large secretory canals in a homogeneous matrix of small fibrous sclerenchyma which is continuous with and identical to the groundwork forming the sporangial walls. Lysigenous tubes lacking, adjoining sporangia having a common tangential wall.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 51. Slide 1629 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Discussion:—

While accurate geological correlation of the horizon of the Des Moines Series producing these and other petrifactions described in this paper is still needed, the evidence of the fossils themselves would tend to indicate a position in the lower part of the series and possibly considerably older than the Carbondale of Illinois. This viewpoint is based on the following facts: Over a period of three years of investigating hundreds of coal balls from Illinois and Iowa (i.e., the Des Moines Series) what appear to be the more primitive plants are all from the latter horizon. *Microspermopteris aphyllum* (described earlier in this paper), with its very primitive habit and psilophytalian characters, is from the Des Moines Series; also *Medullosa primaeva* and *M. Thompsonii*, both of which have been tentatively placed at the bottom of the phylogenetic chart (text-fig. 2) as representing the most primitive stages of the known species. *Dolerotheca sclerotica* and *D. Schopfii*, with their large amount of sclerotic tissue, seem closest to *D. Reedana* which, in being from the Carbondale of Illinois, is the oldest of Schopf's three species. In addition, *D. sclerotica* and *D. Schopfii*, with their much more extreme sclerotic condition, apparent lack of dehiscence tissue, simple lysigenous tubes or complete absence of them, and larger prepollen size (in *D. sclerotica*), seem to indicate an evolutionary stage considerably below that of *D. Reedana*.

Since the much younger *Dolerotheca formosa* shows only isolated groups of sclerenchyma and *D. villosa* appears to lack them completely, the primitive state would seem to have been the almost complete radial septation (of a single telome?) by bands of fibrous sclerenchyma between which were borne the essentially independent radial rows of paired sporangia. If any other proof were necessary to show the radial rather than cyclic arrangement of the sporangia in *Dolerotheca* (Schopf, 1948) it is amply supplied in *D. sclerotica* with its almost continuous radiating network of fibrous-sclerotic bands. In addition, the more numerous and regular bifurcations of the radial framework and the nearly symmetrical intercalation of additional paired rows of sporangia seem indicative of a centrifugal direction of development.

Found in close association with *D. Schopfii* was the *Myleoxylon* fragment shown in fig. 54. A longitudinal section through its outer margin, in fact, shows the base of the fructification with its tissues apparently continuous with those of the petiole (fig. 52). While the continuity of tissues is not so complete as to allow a definite statement as to their connection, the association is extremely close and felt to be worth illustration and mention. If this condition does represent a true attachment it would seem to show that, unlike *D. Reedana*, *D. Schopfii* was sessile and attached directly to fairly large divisions of the rachis.

SUMMARY

1. The known Carboniferous flora is outlined and it is suggested that it falls into large tree-like, microphyllous groups and small shrubby or climbing megaphyllous groups with the pteridosperms being in the latter category. The characters of the pteridosperm stem genera are given, and it is emphasized that they constitute a clearly defined group irrespective of the lack of knowledge as to whether they bore seeds or sporangia.

2. A new unique plant based on a stem with pteridosperm characters is described and discussed. Named *Microspermopteris aphyllum* because of its very small size and leafless condition it offers evidence for the origin of the seed-ferns from the Psilophytales, as well as for megaphyllous leaf development. It combines characters of both *Lyginopteris* and *Heterangium* and appears to have possibly been ancestral to both.

3. Three new species of *Medullosa* are described, and a new phylogenetic viewpoint presented. The evidence for a climbing or creeping habit for the group is given, new evidence being offered for a bilateral, dorsi-ventral habit.

4. Some excellent new material of *Medullosa Noei* is described with particular reference to new data on the conspicuous phloem rays, adventitious aerenchymatous roots, and periderm or "cambial" rings which appear similar to the star rings of the Permian species. "Star rings" are discussed in general, and it is shown that the fourth small stele of *Medullosa centrofilis* had nothing in common with the "star rings" of the Permian plants. "Aggregate leaf traces" in *Medullosa Thompsonii* are described and compared to Permian "star rings."

5. The microsporangiate fructifications of *Medullosa* are discussed and two new species of *Dolerotheca* are described. Evidence is offered that they constitute the most primitive of the known species and show additional proof of a radial rather than cyclic arrangement of the tubular sporangia. A very close association with possible attachment is illustrated for a *Dolerotheca* and *Myleoxylon*. It is also suggested that the plant remains from the Iowa coal balls may be of some aid in a more accurate determination of the horizon of the Des Moines Series.

Thanks are also due Mr. Frederick O. Thompson of Des Moines, Iowa, for his extensive coal-ball collections which provided much of the investigated material, as well as to Dr. J. M. Schopf and R. M. Kosanke, for their cooperation on the *Dolerotheca* section.

BIBLIOGRAPHY

Andrews, Henry N. (1940). On the stelar anatomy of the pteridosperms, with particular reference to the secondary wood. Ann. Mo. Bot. Gard. 27:51–118.
————, (1945). Contributions to our knowledge of American Carboniferous floras. VII. Some pteridosperm stems from Iowa. *Ibid.* 32:323–360.
————, (1948). Some evolutionary trends in the pteridosperms. Bot. Gaz. 110:13–31.
————, and Kernen, J. A. (1946). Contributions to our knowledge of American Carboniferous floras. VIII. Another *Medullosa* from Iowa. Ann. Mo. Bot. Gard. 33:141–146.
Arnold, C. A. (1940). Structure and relationship of some Middle Devonian plants from western New York. Am. Jour. Bot. 27:57–63.
————, (1947). An Introduction to Paleobotany. New York.
————, (1948). Classification of gymnosperms from the viewpoint of paleobotany. Bot. Gaz. 110:1–12.
Benson, M. (1933). On the roots and habit of *Heterangium Grievii*. Ann. Bot. 47:313–315.
Bower, F. O. (1930). Size and Form in Plants. London.
De Fraine, E. (1912). On the structure and affinities of *Sutcliffia*, in the light of a newly discovered specimen. Ann. Bot. 26:1031–1066.
————, (1914). On *Medullosa centrofilis*, a species of *Medullosa* from the Lower Coal Measures. *Ibid.* 28:251–264.
Halle, T. G. (1916). Lower Devonian plants from Röragen in Norway. Kgl. Svenska Vetenskapsakad. Handl. 57:1–43, *pl. 1–4.*
Hirmer, Max (1933). Zur Kenntnis der Structurbietenden Pflanzenreste des jungeren Palaeozoikums. Palaeontographica 77, Abt. B.
Hoeg, O. A. (1937). The Devonian floras and their bearing upon the origin of vascular plants. Bot. Rev. 3:563–592.
Lignier, O. (1908). Essai sur l'evolution morphologique de règne végétal. Soc. Linn. Normandie, Bull. VI, 3:35–62.
Sahni, B. (1920). On the structure and affinities of *Acmopyle Pancheri* Pilger. Roy. Soc. (London), Phil. Trans. B. 210:253–310.
Schopf, J. M. (1939). *Medullosa distelica*, a new species of the Anglica group of *Medullosa*. Am. Jour. Bot. 26:196–207.
————, (1948). Pteridosperm male fructifications: American species of *Dolerotheca*, with notes regarding certain allied forms. Jour. Paleont. 22[6]:681–724, *pls. 104–115.*
Scott, D. H. (1899). On the structure and affinities of fossil plants from the Palaeozoic rocks. 3. On *Medullosa anglica*, a new representative of the Cycadofilicales. Roy. Soc. (London), Phil. Trans. B. 191:81–126.
————, (1914). On *Medullosa pusilla*. Roy. Soc. Lond. Proc. B. 87:221–228.
————, (1917). The Heterangiums of the British Coal Measures. Jour. Linn. Soc. (London), Bot. 44:59–104, *pl. 1–4.*
————, (1923). Studies in Fossil Botany. London.
Seward, A. C. (1917). Fossil Plants. Vol. 3. Cambridge Univ.
Solereder, H. (1908). Systematic anatomy of the Dicotyledons. Vol. 2. Oxford.
Steidtmann, W. E. (1937). A preliminary report on the anatomy and affinities of *Medullosa Noei* sp. nov., from the Pennsylvanian of Illinois. Am. Jour. Bot. 24:124–125.
————, (1944). The anatomy and affinities of *Medullosa Noei* Steidtmann, and associated foliage, roots, and seeds. Univ. Mich., Contrib. Mus. Paleont. 6:131–166.
Thiessen, R. (1920a). Composition and compilation of bituminous coals. Jour. Geol. 28:*pl. 11, fig. 42.*
————, (1920b). Structure in Paleozoic bituminous coals. U. S. Bur. Mines, Bull. 117:*pl. 151, fig. A-B, pl. 152, 153.*
Weber, O., und Sterzel, J. T. (1896). Beträge zur Kenntnis der Medulloseae. Naturwiss. Ges. Chemnitz, Ber. 13:44–143.
Westermaier, M., und Ambronn, H. (1881). Beziehungen zwischen Lebensweise und Structur der Schling- und Kletterpflanzen. Flora 64:417–430.
Wilson, Carl L. (1942). The Telome Theory and the origin of the stamen. Am. Jour. Bot. 29:759–764.
Worsdell, W. C. (1906). The structure and origin of the Cycadaceae. Ann. Bot. 20:129–159.
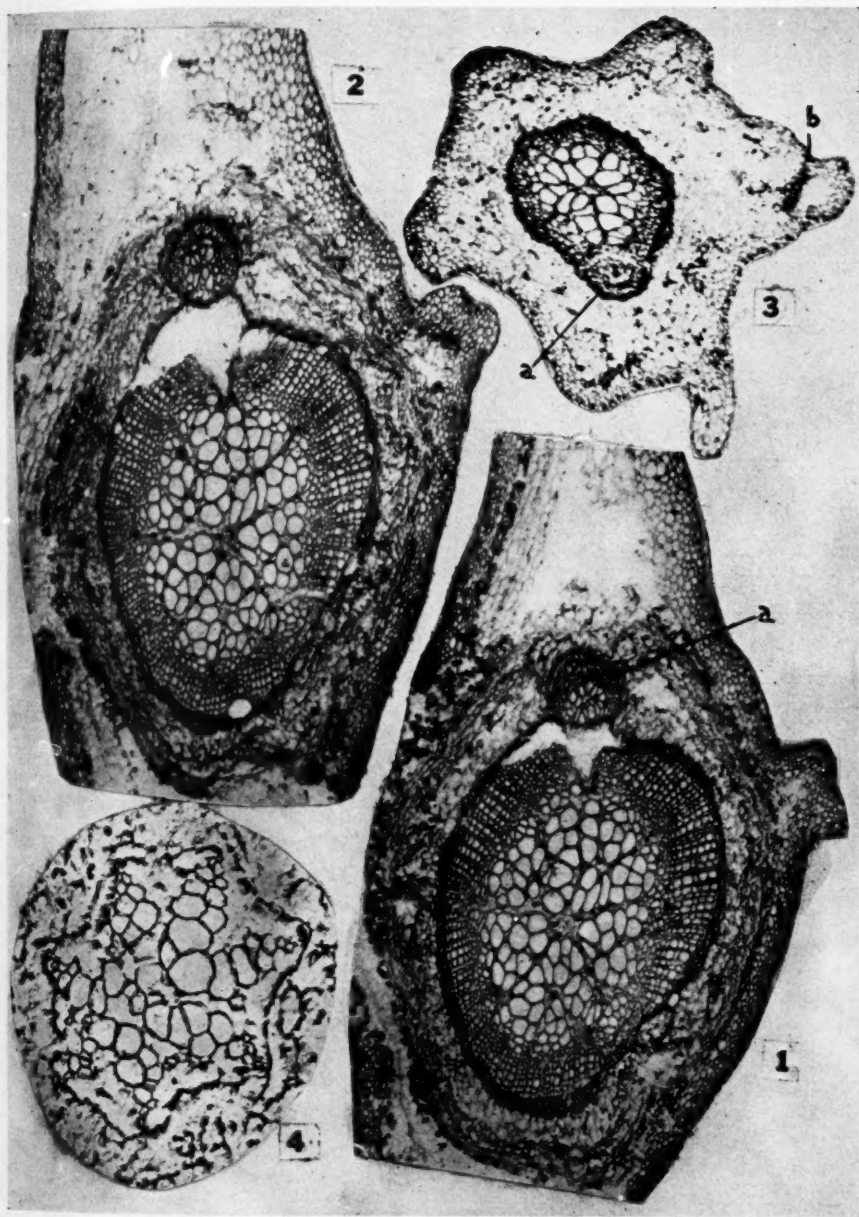
EXPLANATION OF PLATE

PLATE 2

Microspermopteris aphyllum

Fig. 1.   Cross-section of a mature stem showing departure of a collateral branch bundle. From slide 1602, × 20.

Fig. 2.   Same specimen a few peels above the preceding figure. Branch bundle is becoming concentric. From slide 1603, × 20.

Fig. 3.   Cross-section of a small stem (branch?): *a*, beginning of branch vascular bundle departure; *b*, sclerotic plate. (See fig. 55 which shows a later stage of branch bundle departure on same stem). From slide 1604, × 20.

Fig. 4.   Enlargement of the stele of a heptarch adventitious root. (See fig. 56 for appearance of complete cross-section). From slide 1605, × 50.

BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 3

Microspermopteris aphyllum

Fig. 5. Cross-section of same stem as in figs. 1 and 2, showing the horizontal passage of the branch vascular bundle; *a*, forked emergence. From slide 1606, × 18.

Fig. 6. Cross-section taken a few peels above the preceding figure showing departure of an adventitious root; root *(r)* has curved downwards and out of the cortex. From slide 1607, × 18.

Fig. 7. Cross-section of a more mature stem showing unequal xylem development; *a*, sclerotic plate just within the epidermis. From slide 1608, × 15.

BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 4

Microspermopteris aphyllum

Fig. 8.   Radial section of stem: x^2, secondary xylem; *IC*, inner cortex; *OC*, outer cortex; *SP*, sclerotic plate; *em*, emergence.   From slide 1609, $\times$ 50.

Fig. 9.   Tangential view of secondary wood showing small uniseriate rays and pitting in tangential walls. From slide 1610, $\times$ 135.

Fig. 10.   Radial section of stem showing sclerotic plates in outer cortex just within epidermis. From slide 1611, $\times$ 53.

Fig. 11.   Tangential section through outer cortical zone showing anastamosing horizontal plates. From slide 1612, $\times$ 25.

Fig. 12.   Reticulate bordered pitting in wall of a metaxylem tracheid. From slide 1613, $\times$ 450.
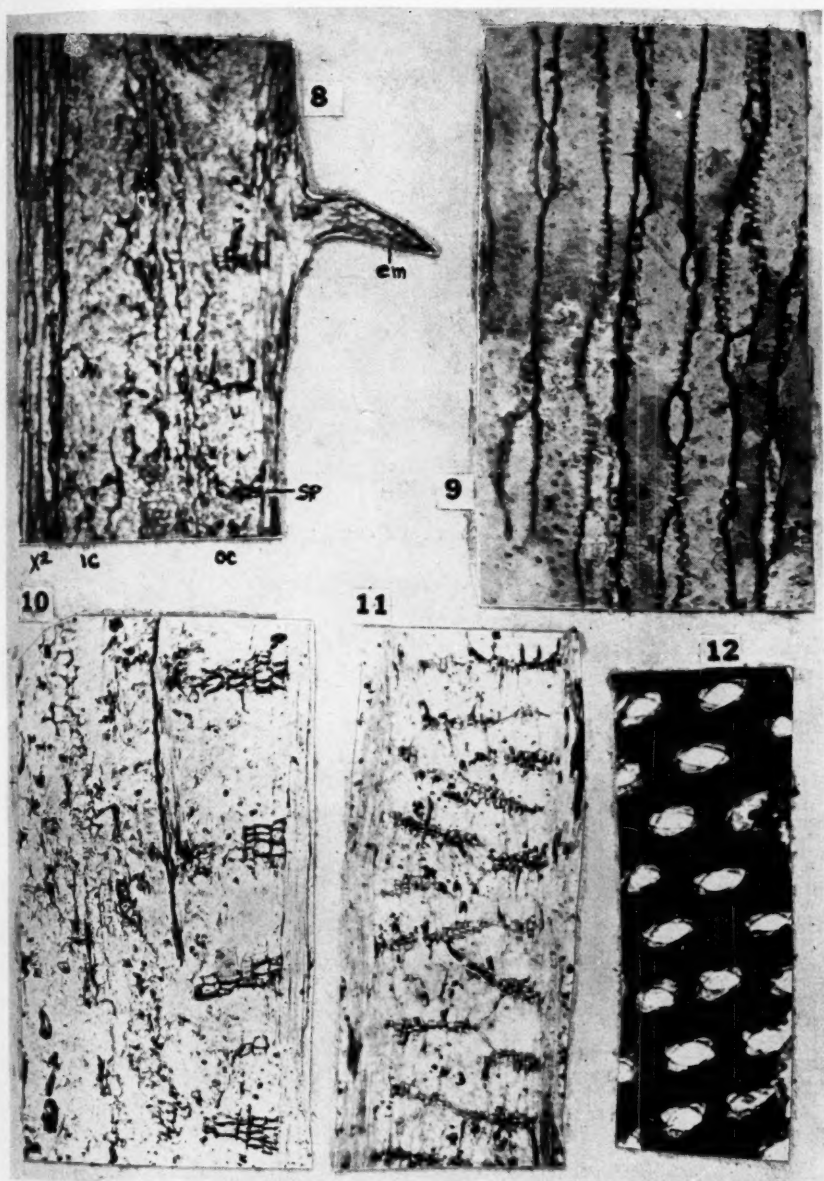
BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 5

A partial reconstruction of *Microspermopteris aphyllum*, × 4. Explanation in text.
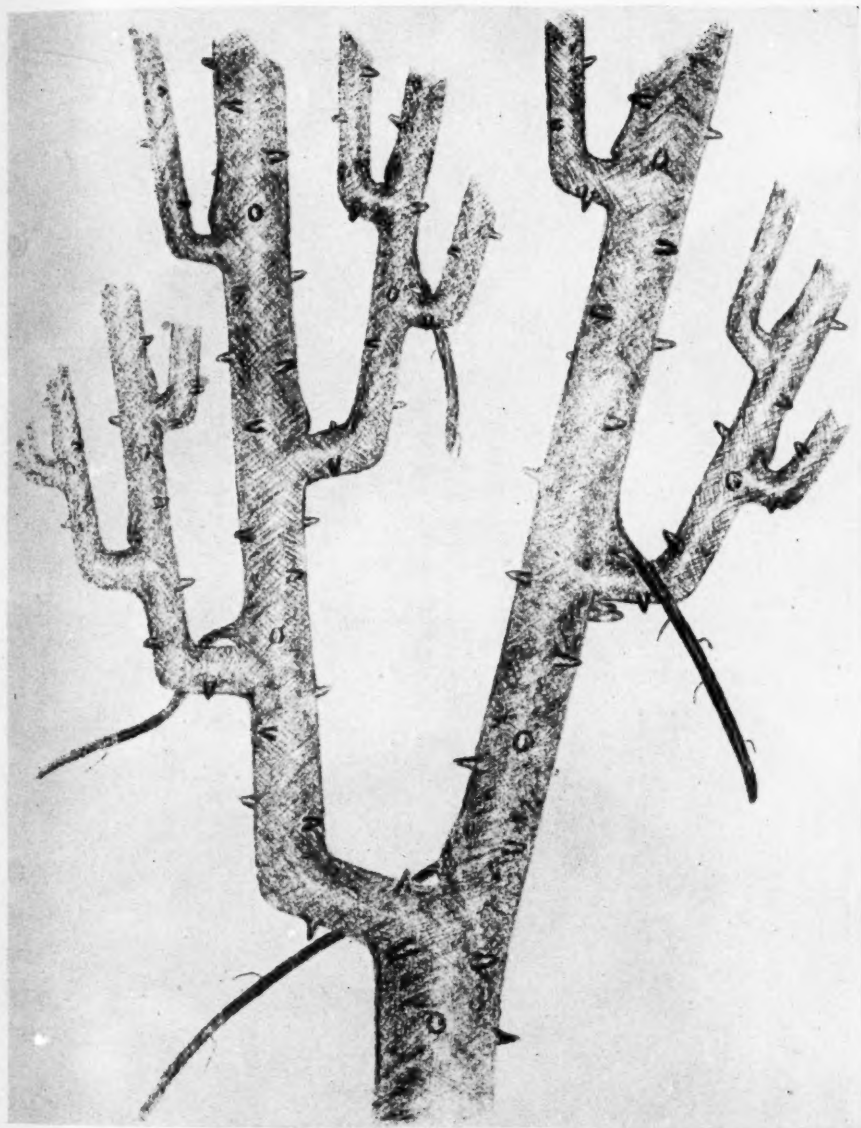
BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 6

Medullosa primaeva

Fig. 13.   Transverse-longitudinal view of type specimen showing branching and fusing of the steles: *a*, small stele in a horizontal course through the stem; $S1$, $S2$, $S3$, and $S4$ show portions of steles indicated in next figure. From slide 1614, $\times$ 4.5.

Fig. 14.   Transverse section of top surface of type specimen: $S1$, $S2$, $S3$, $S4$, $S5$, $S6$, $S7$, and $S8$ indicate the eight steles. From slide 1615, $\times$ 6.2.

Fig. 15.   Transverse section of bottom surface of type specimen. Steles have partially fused. From slide 1616, $\times$ 6.2.
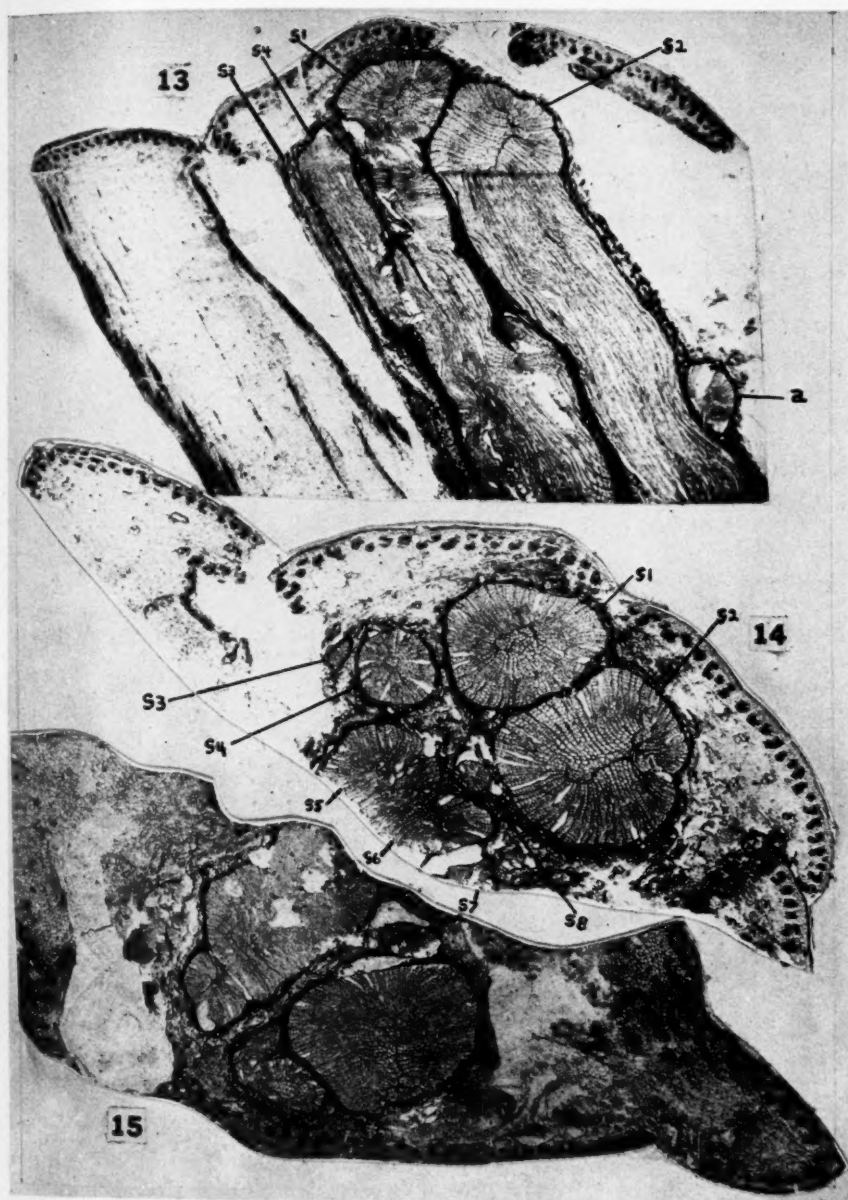
BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 7

Medullosa elongata

Fig. 16.   Transverse view of complete type specimen: *a* and *b*, lateral leaf bases; *c*, dorsal leaf base. From slide 1617, × 2.5.

Fig. 17.   Enlargement of central portion of stem shown in fig. 16 to show the details of the three steles. Note narrow line of primary wood in lower left-hand stele. From slide 1617, × 6.5.

Fig. 18.   Compound resin canals which run horizontally through the stem. From slide 1618, × 6.5.

Medullosa primaeva

Fig. 19.   Enlargement of steles *S1* and *S2* from fig. 14. Note almost solid protosteles. From slide 1615, × 16.
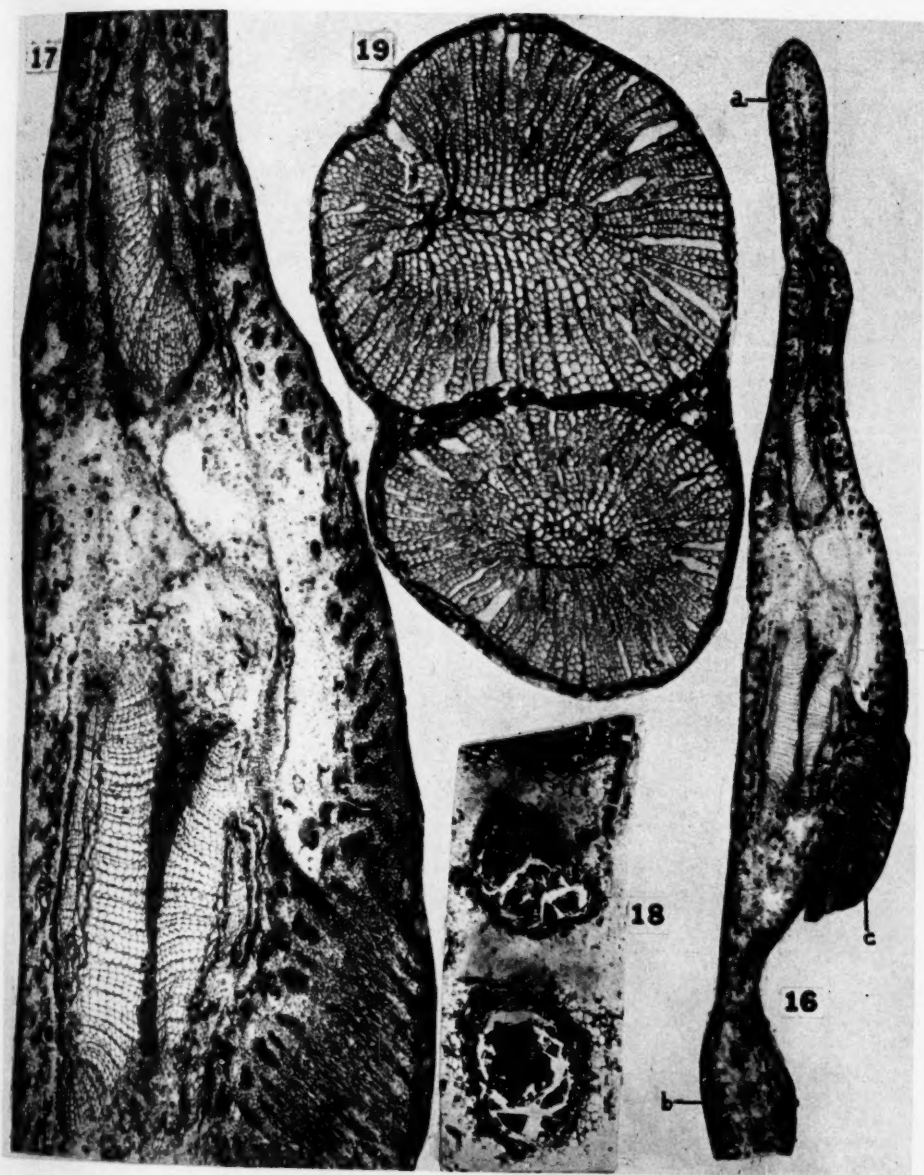
PLATE 7

BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 8

Medullosa endocentrica

Fig. 20. Transverse section of stelar assembly of type specimen with enclosing "periderm": *a*, third small stele; *b*, phloem zone; *XI*, primary xylem. From slide 1619, × 10.

Fig. 21. Transverse-tangential section showing very broad rays in "phloem" area. Above point indicated by *(a)* is transverse, below tangential. From slide 1620, × 40.

Fig. 22. Tangential-transverse section through secondary xylem showing narrow (1–2 cells wide) rays; *a* indicates line between transverse and tangential views. From slide 1621, × 40.

Fig. 23. Portion of a transverse "sieve plate" from one of the large "sieve tubes" of the phloem zone. From slide 1620, × 650.
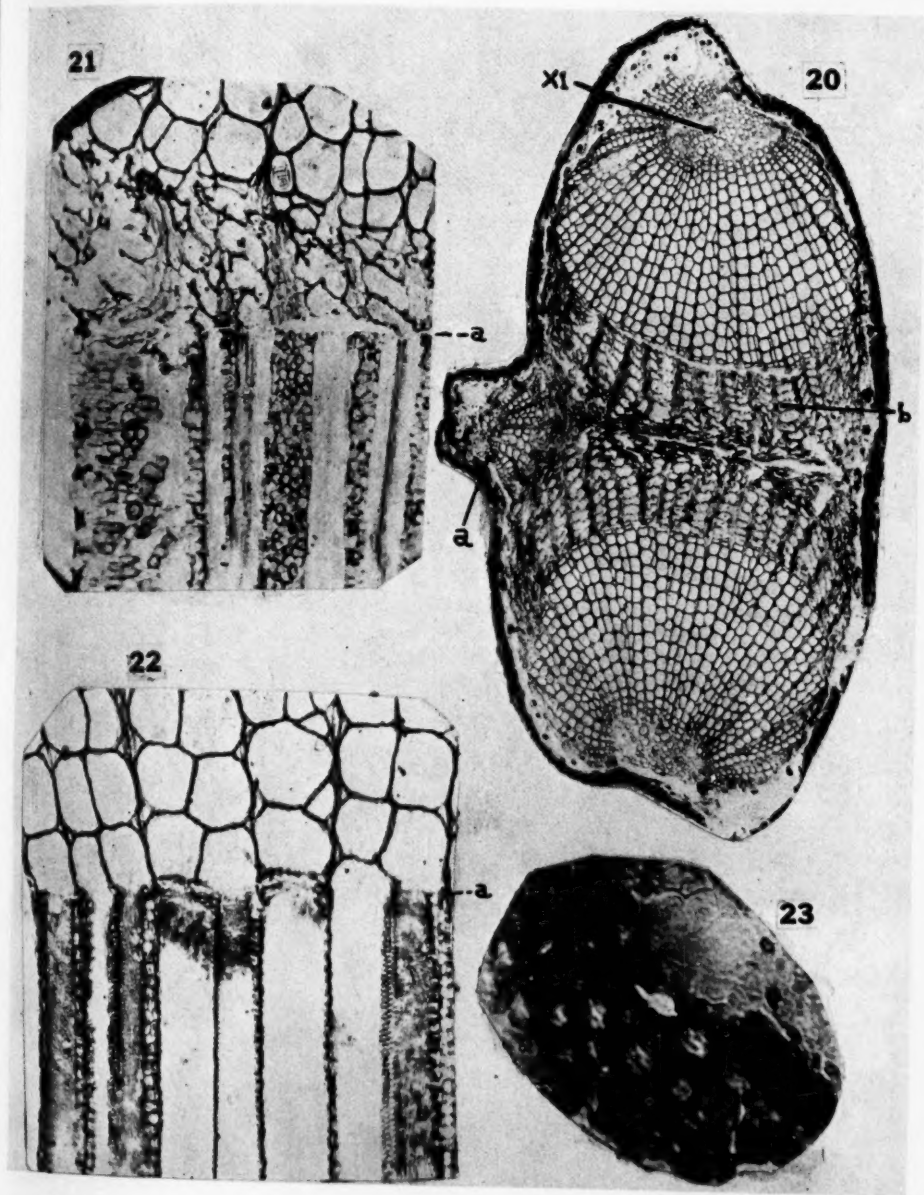
Plate 8

EXPLANATION OF PLATE

PLATE 9

Medullosa Noei

Fig. 24.   A single "cambial ring" showing development of secondary wood. Dark central area is composed of primary tracheids and parenchyma. From slide 1622, × 9.

Fig. 25.   A single well-preserved cortical, pentarch root. Note enclosing periderm and aerenchymatous cortex. From slide 1623, × 14.

Fig. 26.   Marginal portion of a stele showing fringe of expanded phloem rays. From slide 1624, × 12.

Medullosa primaeva

Fig. 27.   Longitudinal section through cortex showing spiral thickening in a leaf trace. From slide 1625, × 95.
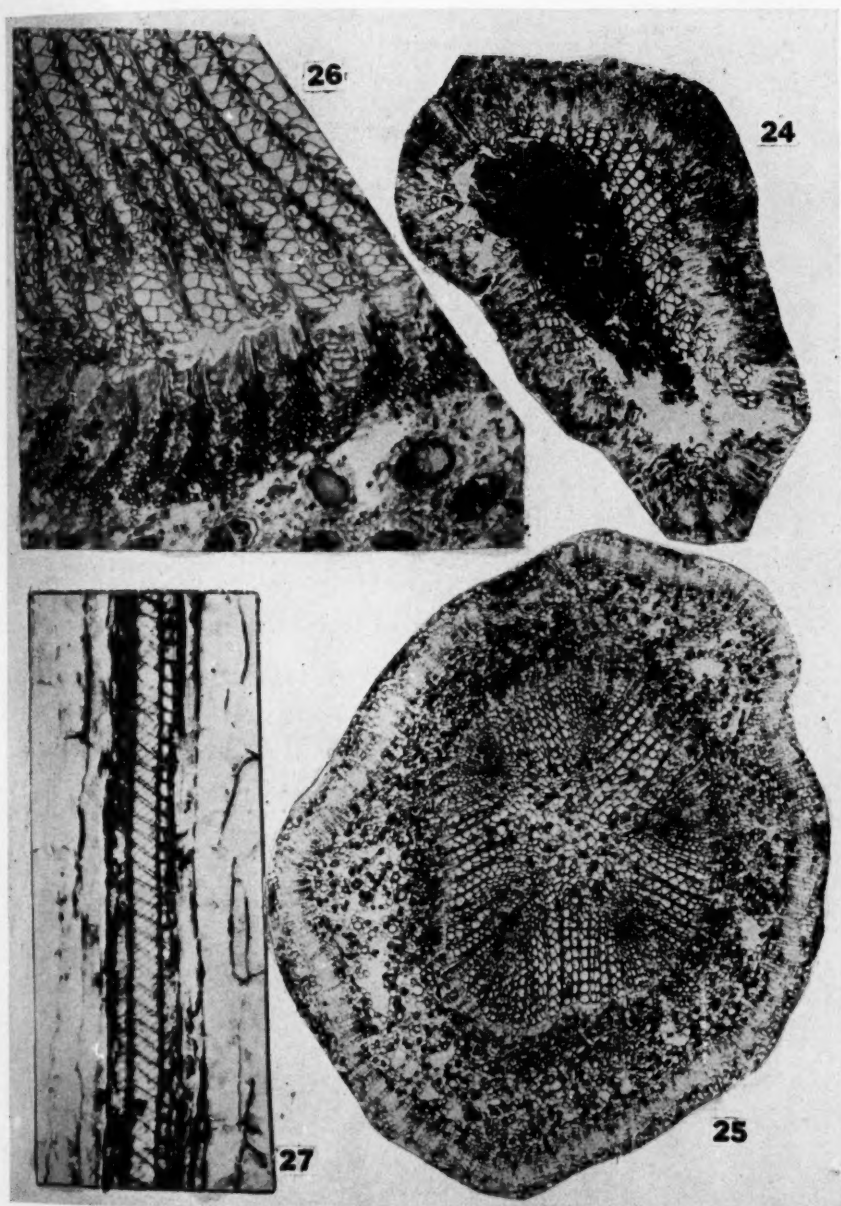
BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 10

"Star Rings"

Fig. 28.   A "cambial" or "periderm" ring from M. *Noei* in which radial rows of secondary xylem have formed. From slide 1622, × 5.5.

Fig. 29.   A "star ring" from M. *stellata* v. Cotta a. *typica*, at the same magnification as the above (after Weber and Sterzel), × 5.5.

Fig. 30.   An "aggregate leaf trace" from M. *Thompsonii* (see fig. 59b).   From slide 1626, × 13.7.

Fig. 31.   A single small stele of M. *primaeva*.   From slide 1615, × 20.7.

Fig. 32.   "Star Ring" of M. *centrofilis* (after De Fraine), × 20.7.
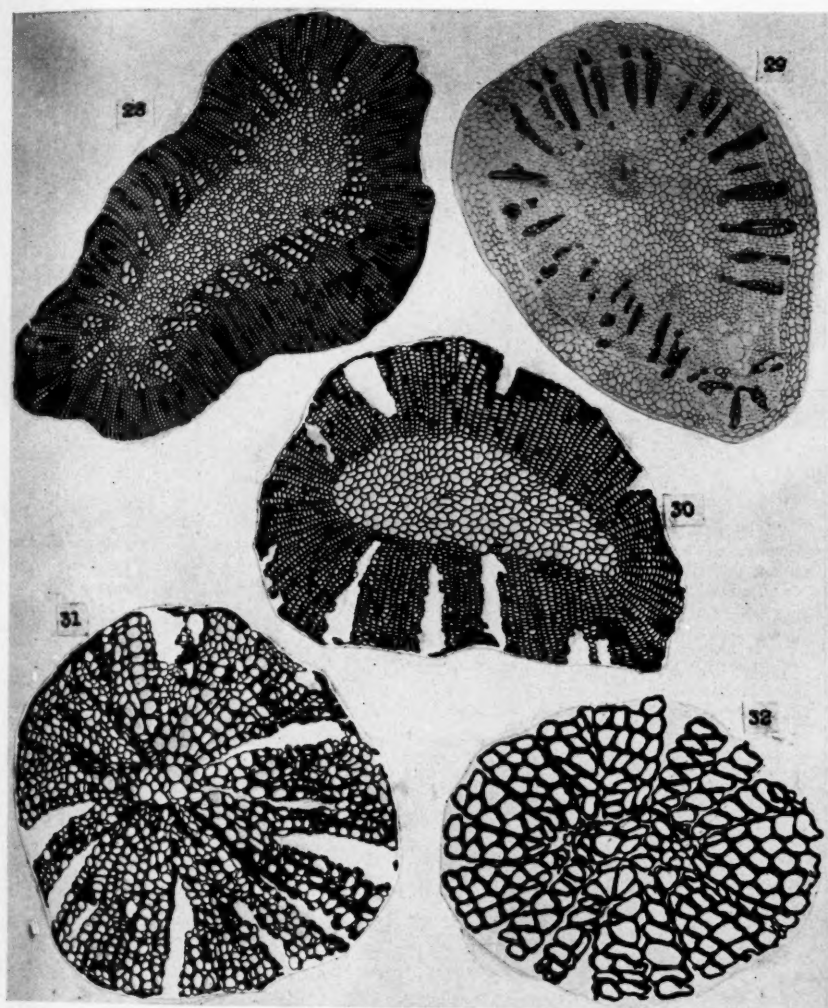
BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 11

Diagrams of the stelar assemblies with enclosing periderm (where present) of all of the Carboniferous species of *Medullosa* with the exception of *M. Leuckarti*. The magnification is 2.8, and all of the diagrams other than figs. 34, 36, 42, and 43 are taken from Andrews (1945, 1946). The primary area of the stele is shown as solid black, the secondary wood as radiating lines, and the periderm as enclosing double or dotted lines depending on whether it was actually observed or was partially assumed.

Fig. 33.   *M. centrofilis* De Fraine; Fig. 34.   *M. primaeva* Baxter; Fig. 35.   *M. Thompsonii* Andrews; Fig. 36.   *M. endocentrica* Baxter; Fig. 37.   *M. anglica* Scott; Fig. 38.   *M. distelica* Schopf; Fig. 39.   *M. pusilla* Scott; Fig. 40.   *M. anglica* var. *Thiesseni* Schopf.
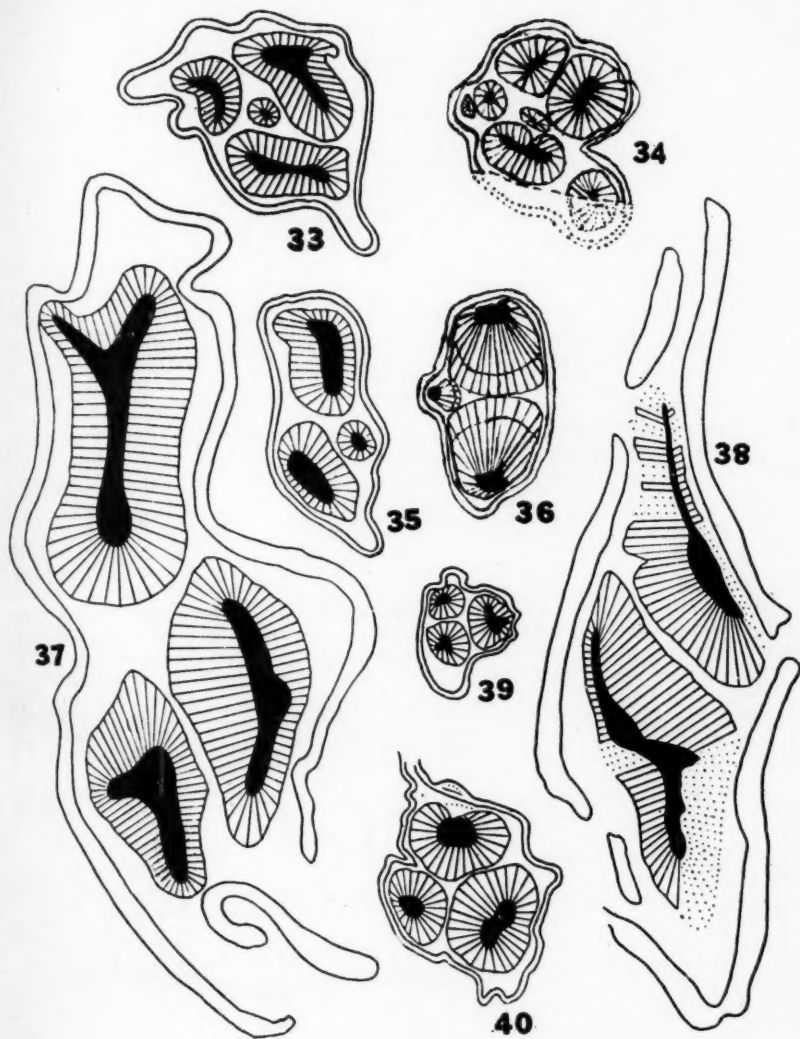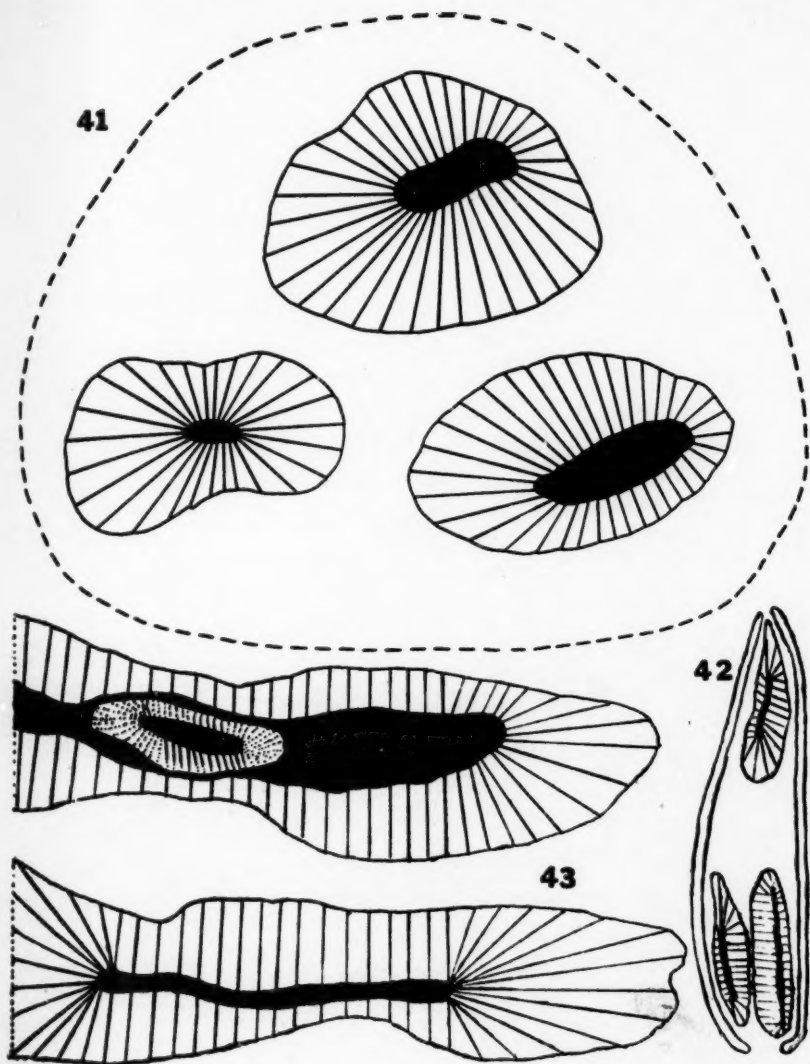
Plate 11

BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 12

Fig. 41.   *M. anglica* var. *ioensis* Andrews; Fig. 42.   *M. elongata* Baxter; Fig. 43.   *M. Noei* Steidtmann, showing only about half of two of the stem's three steles. (*M. Noei* is so much larger than any of the other species represented here that one complete stele at × 2.8 magnification would more than fill an entire plate.) The white ring within the black primary area (in the upper of the two stele halves) represents a "cambial ring" as shown in figs. 24 and 28.
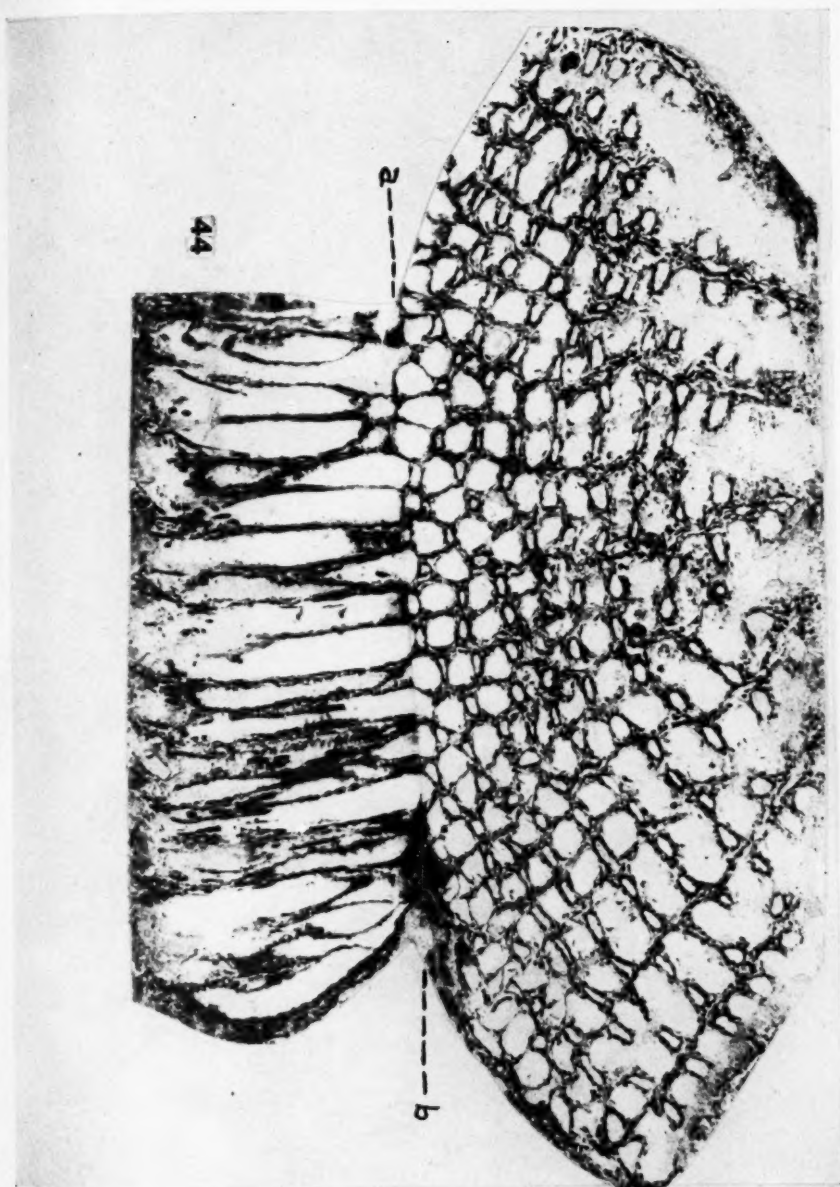
PLATE 12

BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 13

Dolerotheca formosa

Fig. 44. Transverse-longitudinal view of a portion of a complete campanulum. Below the line *a-b* is the longitudinal cut; above, the transverse. In comparison with the following figure note the large lysigenous tubes and absence of a strong sclerotic framework. From slide 1627, × 9.
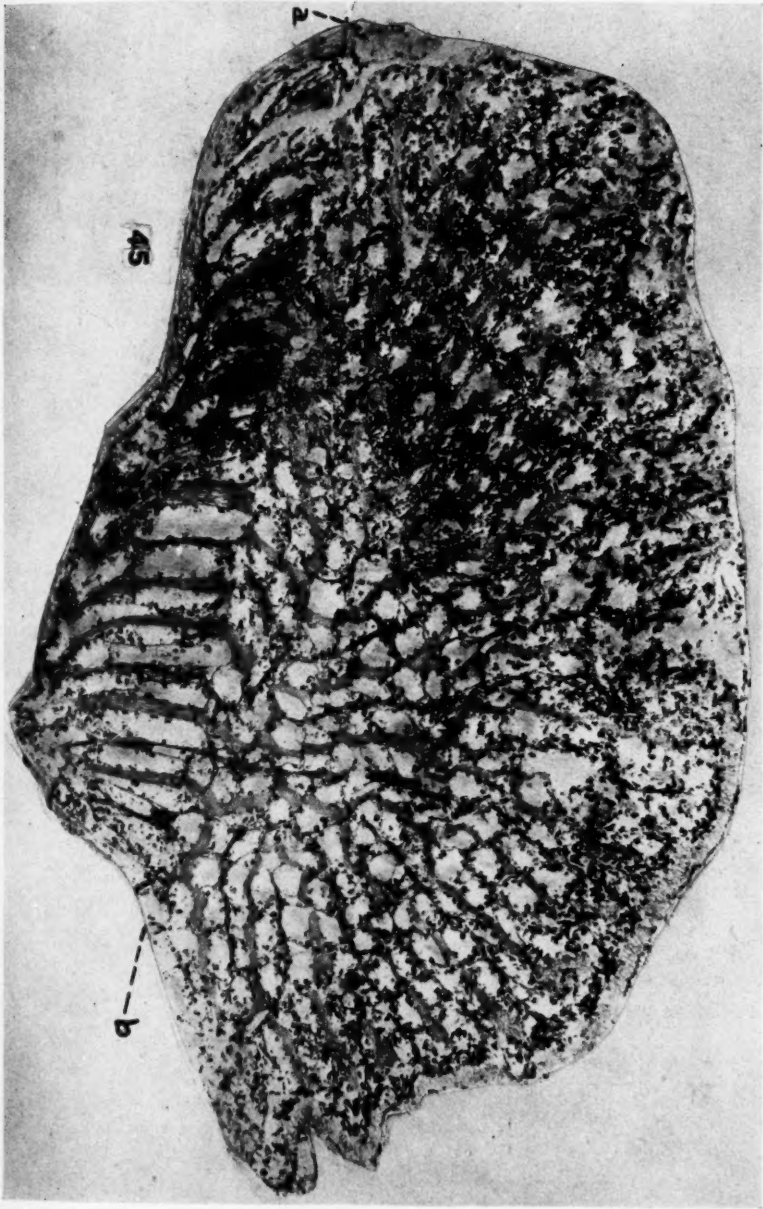
PLATE 13

EXPLANATION OF PLATE

PLATE 14

Dolerotheca sclerotica

Fig. 45. Transverse-longitudinal view of entire fructification. Below the line *a-b* is the longitudinal cut showing the curving of the marginal sporangia; above is the transverse cut showing the bifurcation of the thick sclerotic bands, between which can be seen the parenchymatous-secretory tissue forming the sporangial walls. The upper right-hand margin shows the sclerotic hypodermal zone. For more detailed view see figs. 48 and 49 from slide 1628, × 9.
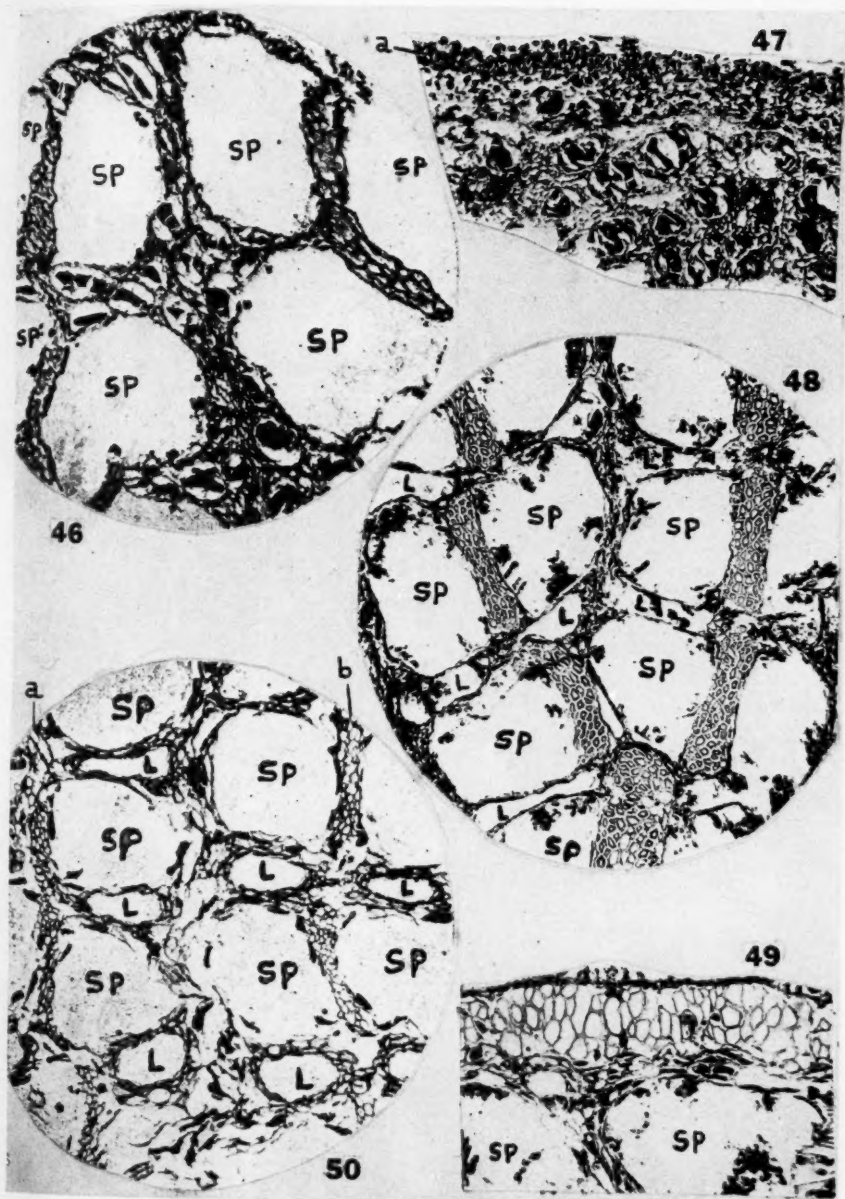
Plate 14

EXPLANATION OF PLATE

PLATE 15

Fig. 46. *Dolerotheca Schopfii*. Transverse view of a double row of tubular sporangia showing four empty sporangia separated by the slime canal and sclerotic ground tissue and enclosed on the left and right by the thick sclerotic bands. Note absence of lysigenous tube between sporangia; *sp*, sporangium. From slide 1629, × 22.

Fig. 47. *Dolerotheca Schopfii*. Transverse view of campanulum wall showing pubescent epidermis and secretory-sclerotic hypodermal zone; *a*, glandular hairs. See fig. 57 for detail of hairs. From slide 1629, × 40.

Fig. 48. *Dolerotheca sclerotica*. Transverse view of a double row of sporangia separated from portions of two other rows by the thick sclerotic bands. Note thin-walled lysigenous tubes alternating radially with the sporangia and bifurcation of the sclerotic bands; *sp*, sporangia; *l*, lysigenous tubes. From slide 1628, × 32.

Fig. 49. *Dolerotheca sclerotica*. Transverse view of campanulum wall showing epidermis and sclerotic hypodermal zone; *sp*, sporangia. From slide 1628, × 40.

Fig. 50. *Dolerotheca formosa* Schopf. Transverse view of a double row of sporangia with the alternating smaller lysigenous tubes. *a* and *b* indicate the much less conspicuous sclerotic bands than in figs. 46 and 48; *sp*, sporangia; *l*, lysigenous tubes. From slide 1627, × 32.

BAXTER—FOSSIL PTERIDOSPERMS
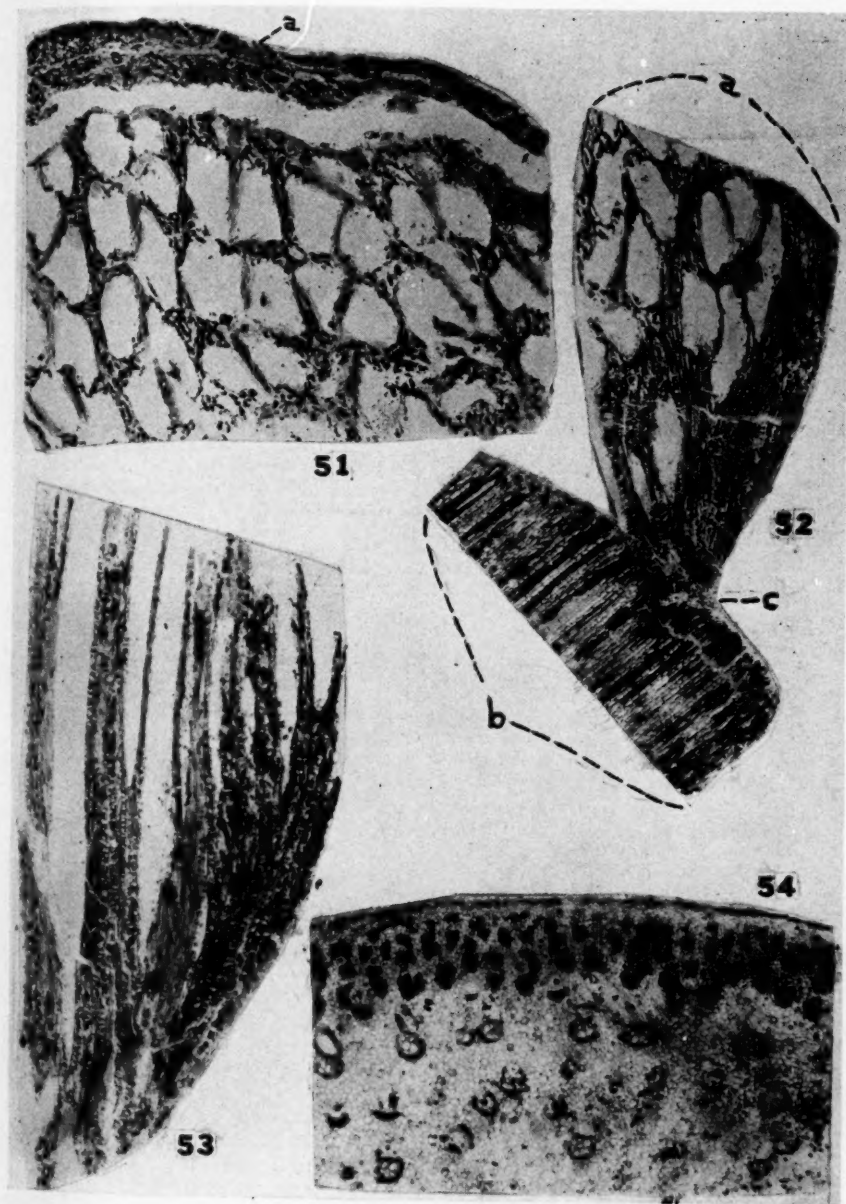
EXPLANATION OF PLATE

PLATE 16

Fig. 51. *Dolerotheca Schopfii*. Transverse view of marginal portion of campanulum: *a*, broad slime canal and sclerotic zone forming the wall of the fructification partly broken away from inner tissue. See figs. 46 and 47 for detail. From slide 1629, × 8.

Fig. 52. *Dolerotheca Schopfii*: *a*, oblique-longitudinal view showing possible attachment to *Myleoxylon* sp. at point indicated by *c*; *b*, longitudinal view of hypodermal zone of *Myleoxylon* sp. shown in fig. 54. From slide 1630, × 8.

Fig. 53. *Dolerotheca Schopfii*. Longitudinal view of marginal portion of campanulum showing the ascending origin of the outermost sporangia. From slide 1629, × 8.

Fig. 54. *Myleoxylon* sp. Transverse view of petiole shown in fig. 52b. From slide 1630, × 9.

BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 17

Fig. 55. *Microspermopteris aphyllum.* Cross-section of small stem or branch showing departure of branch bundle. This represents a stage shortly above that shown in fig. 3. From slide 1632, × 26.

Fig. 56. *Microspermopteris aphyllum.* Cross-section of an adventitious root. From slide 1633, × 34.

Fig. 57. *Dolerotheca Schopfii.* Drawing of epidermal hairs. From slide 1629, × 350.

Fig. 58. *Dolerotheca sclerotica.* Drawing of one of the rare glandular epidermal hairs. From slide 1631, × 550.

Fig. 59. *Medullosa Thompsonii.* Diagram of central portion of the stem: *a,* stelar assembly; *b,* line of "aggregate leaf traces" at point just above the departure of a petiole as indicated by absence of hypodermal fiber strands shown at *c.* See fig. 30 for detail of a single "aggregate trace." From slide 1626, × 4.

PLATE 17
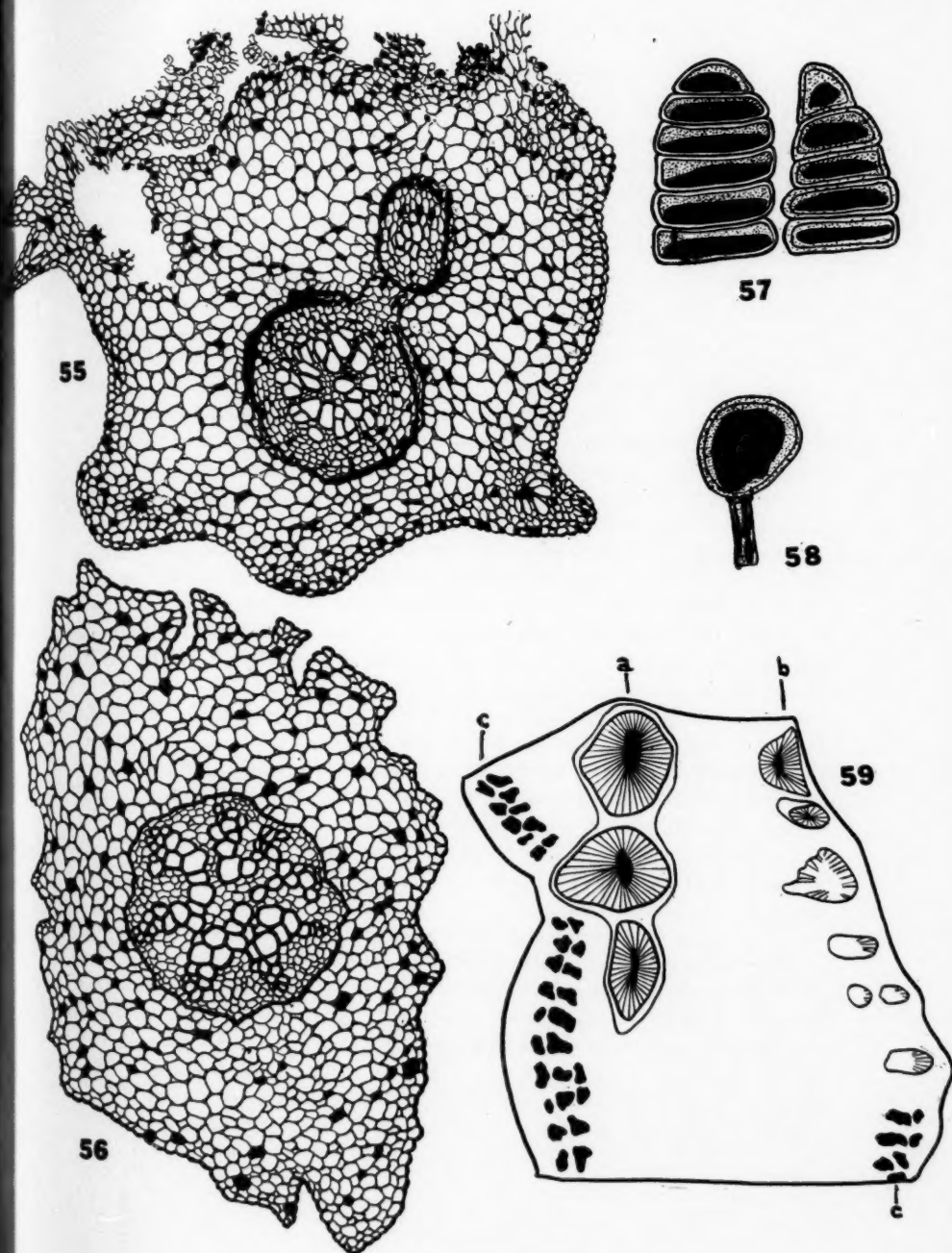
BAXTER—FOSSIL PTERIDOSPERMS
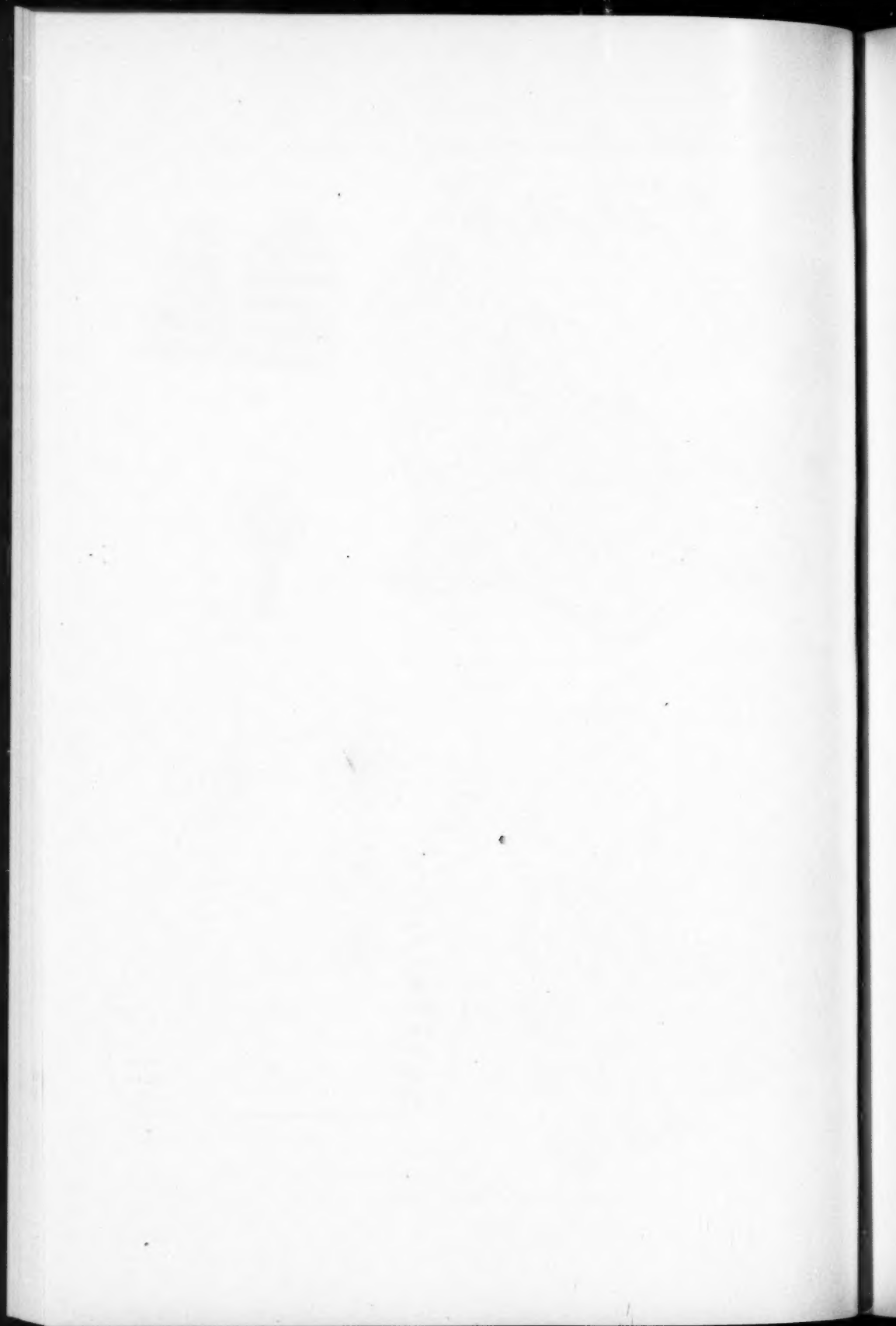
MAIZE AMONG THE HILL PEOPLES OF ASSAM

C. R. STONOR AND EDGAR ANDERSON

INTRODUCTION

Maize is widely grown in the Orient and is used there for a variety of purposes. Authorities once quite commonly believed that it originated there, but the demonstration that it was almost universal in the New World in pre-Columbian times made an American origin seem most likely.   From a meticulous investigation of the historical evidence Laufer (1907) concluded that maize did not reach the Orient until post-Columbian times, and Merrill (1941, 1946) produced convincing evidence that maize and other New World crops had been carried to the Philippines at an early date by the Spaniards and had been widely spread on the continent of Asia. The subject seemed closed and the lack of any evidence for pre-Columbian maize in the Orient became one of the most powerful arguments against any effective trans-Pacific communication in pre-Columbian times.

Several years ago the two authors of this paper came independently to the conclusion that the subject needed to be reopened and examined on its own merits. The senior author, working in the mountains of Assam, found distinctive varieties of maize widely cultivated by the primitive Nagas.   The ethnological and linguistic evidence suggested that these varieties had been in that area a very long time and most probably must have arrived there in pre-Columbian times.   The junior author, having made a beginning at distinguishing between the various races of *Zea Mays* (1942, 1943, 1946), found that the history of maize in the Orient was apparently complex. There was abundant evidence that Merrill was right and that varieties quite similar to those grown in the Caribbean had been brought to the Philippines and Guam by the Spaniards and have since that time been widely spread and extensively grown in the Orient. However, the popcorns, green corns (i.e. those used as a fresh vegetable) and brewing corns did not fit into this picture at all. Almost without exception they are grown by primitive peoples. Their distribution is notoriously spotty and is mostly confined to various ethnological back corners. The Oriental popcorns, furthermore, are not at all like the popcorns of Central America. They are on the whole similar to varieties of maize grown in Peru and Chile in early prehistoric times. As soon as one was able to distinguish effectively between different races of maize, Laufer's conclusions were no longer valid. His evidence can now only be interpreted as showing that maize in the Orient has had a long and complicated history. At an early date the popcorns, green corns, waxy corns, etc., spread widely in the Orient. At a much later date different varieties of field maize were introduced by the Spaniards, and over wide areas are the only type being grown today.

Through the good offices of Dr. W. B. Turrill and Mr. C. E. Hubbard of the Royal Botanic Gardens at Kew, the two authors were put in touch with each other

and since that time have worked together as closely as the distances involved and disturbed world conditions would permit. The collections of native kinds made by Stonor have been grown, pressed, measured, and photographed in Assam. Samples of the same varieties were grown by Anderson at the California Institute of Technology (through the courtesy of Dr. E. G. Anderson) and were pressed, measured and photographed. Pachytene smears were made of each culture with the assistance of Dr. A. E. Longley and Dr. W. L. Brown.

In the following paper the evidence relating to these Assamese varieties, evidence ethnological, linguistic, distributional, morphological, and cytological, is set out as objectively as possible. Part I was written by Stonor, Part II by Anderson. To the authors the conclusion seems inescapable, that there are at least two races of maize in Asia and that one of these must have crossed the Pacific in pre-Columbian time. The direction (or directions) in which it travelled, however, is still uncertain. This new evidence, in other words, tells us little or nothing about the origin of maize. It does, however, enlarge the possibilities which must be considered in any serious investigation of that fascinating problem.

PART I

C. R. STONOR

Before detailing the uses of maize among the hill tribes of Assam, it is necessary to give a very short general account of the tribes themselves and particularly from the angle of their probable origins and directions of migration.

Taking first the tribes of the Assam-Burma border:

1. NAGA TRIBES:—The Naga Hills are inhabited by at least ten tribes, who, although they possess a number of features of culture indicative of common elements in their origin, show many sharp differences in culture, language, traditions, temperament, and physical characters. The Naga tribes are, in fact, more correctly described as the tribes inhabiting the Naga Hills. It is well established that they have elements in their culture complexes indicating wide diversity of origin. There are well-established links with Indonesia, Burma (including the Burma-China border), the Pacific and India. The dominant element today is widely different from any of the main cultures of India, and far more bound up with tribal peoples of Indonesia and southeastern Asia (including Burma). It is certain that there has been continuity of settlement in the Naga Hills for many centuries or millenia. Stone celts are commonly found in the hills, although no tribe today has any tradition of ever having used them. There has probably been a good deal of movement to and from the hills from the Brahamaputra Valley.

2. LUSHAI-CHIN-KUKI TRIBES:—These tribes have limited affinities with the Nagas; and their immediate origin seems to be from hill regions of Burma, where they are closely related to the Karens. There are also undoubted kinships with Indonesia. They are pronouncedly Mongolian and have little or nothing in common with any part of India.

ASSAM
SHOWING THE LOCATION OF
THE HILL TRIBES

SCALE ONE INCH = 32 MILES

3. MANIPUR STATE:—Manipur State is inhabited by a hill population of mixed Kuki and Naga elements, and the big population of the great valley of Manipur is partly derived from these (and particularly the Nagas), and partly from an ancient Mongolian element of uncertain origin.

Taking the tribes of the ranges running east and west and bordering the Brahamaputra Valley on the South in Assam:

1. MIKIR TRIBES:—The Mikir Hills are inhabited by mixed tribes of uncertain origin. There are probably links with both Kukis and Nagas and with the peoples on all sides of them.

2. KHASI TRIBES:—These are classed with the Mon-Khmer group, and their main origin is generally regarded as being the region of Indo-China. It is quite possible that there is an ancient strain in the population akin to the aboriginal stocks of peninsular India and originating from further West. The Khasis are widely different in many respects from the other tribes of Assam.

3. GARO TRIBES:—The Garo tribes have definite affinities with elements among the Nagas and with tribal peoples of the Plains of Assam. There is also some indication of links with Bhutan, and there may well be kinship with parts of India to the West.

Turning to the tribes of the Assam Himalayas lying north of the Brahamaputra:

4. MISHMI, ABOR, APA TANI, DAFLA AKA, MONBA and LAMAI:—The tribes of the Assam Himalayas, divided extremely roughly into Mishmi, Abor, Dafla, Apa Tani, Aka, Monba and Lamai as the main groups, have been very little studied. There has undoubtedly been much migration from the east and I am of the opinion that a big element in the population is akin to the Kachin peoples of northern Burma. There are marked cultural similarities with the Naga tribes, mainly among the Abors. There has been infiltration down river valleys from Tibet and very possibly in the reverse direction into the hills from the Brahamaputra Valley. The Monbas, a small tribe living near the Bhutan border, may have originated from that state.

Even these meagre notes show the hill tribes of Assam to be as mixed a population as can well be imagined, who are linked with literally every part of Asia. Prehistoric (?) stone celts are found throughout the hills, indicating very ancient population. These celts are recorded in the literature from all hill areas south of the Brahamaputra, and I have celts in my possession from the Abor and Dafla Hills of the Outer Himalayas.

Except for the Angami Nagas, the Apa Tanis and the Monbas, and to some extent the Khasis, the basis of subsistence economy is still dry cultivation, carried out by cutting and burning the forest and raising crops for one or more seasons in the area so cleared. The main subsistence crop in the majority of cases is rice, but millets, Job's Tears, sorghum, maize, are all important and are grown in varying amounts by nearly all tribes. In a few instances, one or other of these cereals is as important as rice, as, for example, among the Abor tribes, who grow rice and Job's Tears in almost equal amounts, or the Chin tribes of Burma and the Monba tribe of the Bhutan Border, who grow more maize than they do rice. It seems probable that the complex of Job's Tears-millets-maize preceded rice as the main food supply of many tribes.

In general, the tribal peoples of the Assam mountain tracts live in the so-called Neolithic stage of culture. The community is a self-contained one, growing its own food, weaving its own cloth, regulating its own affairs by tribal law. There is no writing, and the religion is animistic. The level of culture is very similar to the tribes of Borneo, the mountain tribes of the Philippines, and some at least of

the South American Indians. In the Naga, Lushai, Khasi, Mikir and Garo hills there has been missionary activity for some decades, and the tribes have been administered for the same period, so that far-reaching changes have set in. This is not, however, of consequence for my present purpose, the more so since administration has done remarkably little to change or to develop the economic life. In the Himalayan tracts north of the Brahamaputra, administration has only been started since the end of the War. Missions are banned from entry, and large tracts are still unexplored.

DETAILS OF VARIETIES, CULTIVATION, USE, ETC., OF MAIZE AMONG THE HILL TRIBES OF ASSAM

The notes which follow are all based on information obtained at first hand in the field, either by direct observation or questioning members of the tribes concerned, or more usually by a combination of both. Where I have had to rely on the work of others, or have not visited an area, I have drawn attention to the fact.

1. ANGAMI NAGAS:—   (

Varieties grown: Nos. 5–18, particularly the larger flint types.

Ecology and technique: The Angami Tribe lives in hills from 2500 to over 6000 feet in altitude. The great bulk of the tribe lives above the 4000 feet level and in a sub-temperate climate. Maize is universally grown, and the larger flint types predominate. The Angamis have a remarkable system of irrigated rice-cultivation, and only a small proportion of their crops is grown on dry fields. Maize is grown mixed either with millet and Job's-tears or else as a pure crop, usually in small plots in the immediate vicinity of the village. Sowing is by dibbling.

Uses: Their irrigated rice-cultivation leaves the tribe well provided for. Maize, along with millets and Job's-tears, is important for human consumption mainly among poorer people who are short of rice fields. It is, together with subsidiary crops (notably millets), a catch-crop to "fill up corners" before the rice is harvested. It is eaten fresh, either boiled or slightly roasted, and is largely consumed by children. The main use among this tribe, in years of good harvests at least, is for *pig feed*, the grain being parboiled and roughly mashed. It is only so used when actually in season, and is not stored for feeding the pigs. Small quantities of the popcorn types are stored for popping, but this is not important. It is used occasionally as an ingredient in beer, along with other cereals.

Storage: The ears are hung up on the rafters of the dwelling house for next season's seed.

Folklore, traditions, etc.: The Angamis I have talked to simply state that they have grown maize from time immemorial. The tribal name of corn is *Tsüke*.

2. LHOTA NAGAS:—

Varieties grown: The varieties grown in the village of Yimbang at elevations of less than 2000 feet in the sub-tropical lower ranges of the area are:

   1. *Tchetum-sopfu* (Serial L. 1), meaning "Small late," regarded as an indigenous variety.

2. *Moro* (Serial L. 2), meaning "Quick or early eating," regarded as indigenous.

3. *Aorr-chemyang* (Serial No. 6 of first consignment), meaning "Ao Nagas blood." This refers to traditional origin from the neighbouring Nagas, the term blood having reference both to the small red grains, and to the former enmity between Lhotas and Ao's.

4. *Konoma-tsunghundhro* (Serial No. 8 of first consignment), meaning "Konoma Maize," the name Konoma being that of a large Angami Naga village to the south of the Lhota country, and indicating that it probably derived from there. A very similar type is known as *Wokotsu*, because it was first got by Yimbang from a Lhota village of that name.

5. *Epuk* (Serial No. 12 of the first consignment), meaning "Bursting," as it is only grown for popcorn.

6. *Kor-chak*, meaning "Horse-Food." This variety, a coarse flint maize grown in many parts of India, was obtained within living memory from Nepalese immigrants into this region. The name is derived from the custom of the Nepalese of keeping ponies.

The main varieties grown in the village of Yekhum, in the higher areas of the Lhota country and almost within sight of Yimbang, where conditions are between sub-tropical and sub-temperate and the altitude about 4,000 feet, are only two: (1) *Korchak* and (2) *Konoma-tsunghundhro*. Both are said to be of fairly recent introduction, and supplanted other types. Other types may be grown in small amounts.

Ecology and technique: A great part of the Lhota Naga country is sub-tropical, and there are few villages situated over 4,000 feet. The types grown are naturally those most suited to this climate. Maize is grown as a mixed crop among the rice and subsidiary cereals. It is commonly sown in rows along the edges of field paths or inter-field boundaries. The seed is dibbled, and the sowing season is March–April, while the harvest is from June to early August.

Uses: Maize is not a very important crop among the Lhota Nagas and, as among the Angamis, it is grown wholly as a catch-crop, utilized before the rice harvest is in. But it is grown entirely for human consumption, and except for the popcorn *Epuk* variety, it is entirely consumed as it ripens. A little is used now and again for beer-making. The reasons for growing the different types is gone into in more detail below.

Storage: The ears for next season's seed are simply hung up on the rafters of the dwelling house.

Traditions, folklore, etc.: The general word for maize is *Tsunghundhro*, which means "something obtained from the Angami Nagas," and I have been told of a vague tradition that the Lhotas first got maize from their Angami neighbours. On the other hand, the variety *Tchetum-sopfu*, listed above, is regarded by the Lhotas as their own maize and does not seem to be grown by the Angamis.

The Lhotas have been in their present country for a matter of centuries. They state that they have had maize from time immemorial.

3. AO NAGAS:—

Varieties grown: Some or all of Serial Nos. 5–18.

Ecology and technique: Closely parallels that of the Lhota tribe.

Uses: As among the Lhotas, it is entirely for human consumption.

Storage: As for the Lhotas.

Traditions, folklore, etc.: The Ao Nagas have a tradition that they have always grown maize among their field crops. The usual name for maize is *Mentia*, for which I can get no translation. A small group of villages which have a different language know it as *Achang-Tangba*, which means "bearing rice already husked." A curious local name has been recorded by J. P. Mills ("The Ao Nagas," 1926. p. 125, footnote) as used in the Ao village of Changtongia: *Moya zungkhum*, meaning "Sema Naga Lentils."

4. SEMA NAGAS:—

Varieties grown: Some or all of Nos. 5–18.

Ecology, technique, etc.: Very much as for the Lhotas and Ao's, except that maize is a much more important crop and is planted thicker on the ground. Sown during March–April, and harvested in June–August.

Uses: Is of considerable importance for human consumption, both fresh on the ear and (to a lesser extent) stored and pounded to mix with rice. It is also used to make several types of strong beer, again to a greater extent than among other Naga tribes. My information from the Sema area is scanty. However, the importance of maize is very likely linked with the shortage of land for cultivation and the large population of poor people, so that the staple food of rice is apt to be finished well before the next harvest. Catch-crops are consequently of much importance, and rice insufficient for beer-making.

Traditions, folklore, etc.: The Semas regard maize as an ancient crop. The name for it is *Kolakithi*. This is usually translated as "Foreigner's Job's-tears," and some Europeans have assumed without evidence "Foreigners" to mean the British and that maize was introduced into the Naga Hills by the British (!). Apart from this, I have been given another meaning for the word by a Sema Naga: "Grain that is eaten by plucking singly." Another word is *Amehukethi*, meaning "a grain ripe and eaten before the rice."

5. CHANG NAGAS:—

Varieties grown: Some of Nos. 5–18.

Ecology, technique, etc.: As for other Naga tribes. Most of the Chang Naga country is high and cold with sub-temperate climate, and the larger coarser flint types predominate. A small popcorn (Serial No. 12) is grown, and the African dent maize is also cultivated.

Uses: Except in a few low-elevation villages, the Chang Nagas even today depend largely for their subsistence on millets, Job's-tears, maize and taro, rather than rice. Maize is thus an important crop. It is, however, largely a catch-crop, eaten fresh, but appreciable quantities are stored and are mixed with other cereals for food during the cold weather. It is used preferably in making beer, and to a small extent for popcorn. Some, particularly in seasons of good harvest, is fed to the pigs.

Storage: In round baskets, stripped from the cob, in separate granaries.

Traditions, folklore, etc.: The Chang name for Maize is *Hangi,* for which I can get no translation. It is certain from their traditions and recent history that the Chang Nagas have been pushing west from the Burma side for some generations, and they themselves claim that at least a large element in their composition came from further east. Their economy is as noted, still based very much on Job's-Tears, millets, and maize. This is partly due to their living largely in high altitudes and possessing no suitable type of rice for the climate; but I have several times been informed by Changs that it is only since they have had contact with the more westerly Naga Tribes that they have taken to rice at all; and rice is widely recognized as being a more recent crop than the other cereals, maize not excluded. Among this tribe each major crop has its own minor tutelary deity, maize among the rest. The African dent maize is known as *Bilati Hangi,* meaning "English Maize."

6. YIMCHUNGRR, KONYAK and KALYO-KENGYU NAGAS:—

I have very little information from any of these tribes. Maize is grown in varying amounts by them all. It is said to be an important crop among the Kalyo-Kengyu, but not very much grown among the Konyak Nagas, who are among the most ancient stock in these hills. I have visited the extreme northeast area of the Konyak country, where a poor type of one of the larger-grained flint maizes is grown in small quantities. I was told that the people were not keen on it as it attracted bears to the fields. The Konyak name for maize is *Tongi.*

7. KACHA NAGAS and NZEMI NAGAS:—

These two closely allied groups inhabit the southern Naga Hills. I have been there once and can confirm that maize is grown in the fields along with other cereals, and my original stock of small-grained types came from this area. The area varies a great deal in elevation (from 1,000 to 7,000 feet) and most or all of Nos. 5–18 are grown.

I have a rather vague report from a Government subordinate concerning a branch of the tribe living in the hotter areas, about 3,000 feet, that three main types are recognized: (1) *Imbaume mei Mitak,* early; (2) *Lingtak,* second to ripen; (3) *Lingtak tiingne,* late. The first two are said to be the most widely grown.

The Kacha Nagas have a tradition that the tribe first emerged from a cave in their area, and brought their old established crops with them, maize being among them. I have no details of its use except that most or all the crop is used as it ripens and is not normally stored.

8. SANGTAM NAGAS:—

There are two geographically separated branches of this small tribe. I have visited the northern branch.

Varieties grown: I have obtained the following list and notes from a Government subordinate, himself a member of the tribe.

1. *Chemese,* sown in March and harvested June to July.
2. *Mesease,* meaning "sweet maize." Is regarded as good for making beer and is grown mostly in rocky fields.
3. *Nurachese,* a small popcorn maize.
4. *Hengchimerem,* used both for human consumption and for pig feed.
5. *Yengchengese,* used mainly for beer and for pig feed.
6. *Ahochese,* not regarded as very good, but grown as it is ripe earlier than the rest.

Unfortunately, my small collection from the northern Sangtam area got rather mixed and labels lost. I can, however, note that of the above No. 2 is a small red-grained type similar to but larger than Serial 6. No. 2 *(Mesease)* is a very small white-grained popcorn identical with Serial 12. No. 4 *(Hengchimerem)* is a fair-sized maize with large, coarse grains, and a proportion at least are red. No. 6 *(Ahochese)* is a stout rather coarse type with large hard yellowish-white grains.

Ecology, technique: The northern Sangtams live in steep country, and grow their maize mixed with millet in their ordinary fields.

Use: The above list shows the main use of maize and I have little to add. Most is said to be eaten when soft, but a proportion is stored for the winter, when its main use, except in seasons of rice shortage, is for beer. It is a fairly important catch-crop, probably more so than among the Ao and Lhota Nagas. Much of the Sangtam area (as among the Chang Nagas) is high and cold and unsuited for rice growing.

Storage: In baskets, after shelling, in the granary.

Folklore, traditions, etc.: The Sangtams simply informed me that they have always had maize among their crops, as far back as their traditions reach.

9. RENGMA NAGAS:—

I have never visited this little tribe, which is split into two geographically separated parts, of which the eastern branch is very primitive. Writing of the eastern Rengmas, J. P. Mills ("The Rengma Nagas," 1937, p. 86) states:

> On the *jhum* maize is a far more important crop than it is in the Western Rengma country. It is both eaten boiled and used for brewing. Ordinarily it is sown scattered among the Millet *(achota,* the Sorghum) with which it is harvested, but some men grow whole fields of it.

Of the western branch of the tribe, the same writer says (l.c., p. 77): "Maize —though an important crop among the Eastern Rengmas, is little grown by the Western Rengmas. At most a few plants are grown among the rice and the heads roasted and given to children to eat. Occasionally a brew is made from it nowadays, but the resulting beer is not popular." The words for maize are (both from Mills): Western Rengma—*Samphuruchi*, and in Eastern Rengma—*Akhuzi*.

Mr. Mills has recorded from the Eastern Rengmas (p. 88):

Early in August there is a series of five "genna" days. The first day is called *Atsetatsate*, and is held to prevent waste of food. The next four are called *Tsate*, the festival of formal first fruits, that marks the beginning of the maize and millet harvest. Young men go to the fields and bring back leaves of millet, which only the women eat, or pretend to eat raw. Men also bring in Maize-heads that day. These are not eaten that day, but kept till the next day but one following, when everyone eats roasted Maize. Throughout this "genna" all work ceases and people entertain their friends at drinking parties.

10. THE LUSHAIS:—

Varieties grown: L1–L8 as sent. A list of the types grown, as sent me by a reliable government subordinate is:

1. *Ralte Vaimin* (Serial L1), regarded as indigenous.
2. *Pawi Vaimin* (Serial L5), meaning "Chin Maize."
3. *Sap Vaimin*, meaning "European Maize." This variety is a dented maize recently introduced by the British.
4. *Bawngpu Vaimin* (Serial L7), meaning "Herdsmen's Maize." This is a large coarse flint maize introduced by Nepalese immigrants (the "Herdsmen").
5. *Chingzo*, meaning not given.
6. *Vai Vaimim* (Serial L4), meaning not given.
7. *Lenliam* (Serial L6), meaning not given.
   Nos. 5, 6, and 7 are regarded as similar, and have small, dark-grained ears noted for the stickiness of the grain while soft.
8. *Puakzo* (Serial No. L8), meaning "Burst all," as it is grown for use as popcorn.

Ecology and technique: I have not visited the Lushai Hills, but have first-hand information that, as among the Nagas, maize is grown among the other crops in the dry *jhum* fields, and occasionally as a pure crop. In the latter case I am informed that it is usually followed by a legume crop. The seed is dibbled, and the sowing season is said to begin in April, with the harvest from July to August.

Uses: The bulk of the crop is eaten, boiled or roasted, as it ripens, and is thus a catch-crop as among the Naga tribes. It is also used to some extent as pig food, and a little fed to poultry. Limited amounts are stored (presumably by poorer people, and in lean years), and the grain is roughly pounded and mixed with rice. The small *Puakzo* is probably grown entirely for popcorn. I have no information of maize being used for beer, and I think it to be so used very seldom. Some of the

Lushais in the high-altitude eastern areas with a cold climate use maize as a main crop; this is due to lack of a high-level rice, and will be described under the Chin tribe.

Storage: I have no information.

Traditions, folklore, etc.: Lt. Col. J. Shakespear ("The Lushai Kuki Clans," 1912, p. 87) states that there is a festival known as *Mim-Kut,* named after the Maize, as it takes place when the crop ripens. It is of but little importance and seems likely to die out. Cakes of Job's-tears are eaten, and the next day is *brilh.* N. E. Parry ("A Monograph on Lushai Customs & Ceremonies," 1928, p. 91) refers to this feast as being in honor of persons who have died during the past year. He mentions that the "Fresh vegetables, maize, bread, necklaces, & cloths are placed on the memorials of the dead."

Shakspeare remarks of the chiefly clan of Fanai, who originated from the Chin country to the East (l.c., p. 139): "A dead Fanai is buried in the usual Lushai way, but no rice is placed in the grave. An offering of Maize is however suspended above it. It may be noted that in the Zahao country rice is not cultivated, the staple crop being maize."

It is possibly an exaggeration that maize is the only main crop in this area: but I have had it confirmed by members of the Lushai tribe that it is more important than rice.

11. THE LAKHERS:—

I have not visited this tribe, which lives next to the South Lushais. Their system of cultivation is the same as among the Lushais, and it is reasonably certain that maize is grown in the same way, and is of the same importance. The Lakher word for Maize is *Chhamei.* Rice is the staple crop. A minor use of the dry grain is mentioned by Mr. N. E. Parry ("The Lakhers," 1932, p. 199), who states that it is used for counting. The same authority describes a very interesting dance performed in one village in connection with the maize harvest (l.c., p. 434):

> In Chapi village, to celebrate the gathering in of the Maize harvest, a dance called *Pazutawla* is performed. The men hold hands and form a ring; the girls stand in front of them; one girl stands between two men, and puts an arm around the shoulders of the men on each side of her. They dance round and round, singing to the accompaniment of gongs and drums. The dance is peculiar to Chapi. It is *ana,* to dance it except in celebration of the maize harvest, and were it performed at any other time those taking part would suffer from carbuncles.

12. THE CHINS:—

In the Chin Hills, which are politically within the borders of Burma, maize is a very major crop. All my information is from "The Economics of the Central Chin Tribes," by H. N. C. Stevenson (1943).

Stevenson lists maize as among the staple crops (p. 35) and states that it is grown along with millets and beans. The system of cultivation is as a mixed crop in the *jhum* fields. The ears are stored, hung from the rafters of the dwelling-house. He implies that it is of equal importance with rice. It seems to be used

both fresh and after being stored; it is used, mixed with rice and millet, for beer-making.

Stevenson gives interesting notes on uses of stored maize. Thus under "Travel Rations," which he describes as being the most common form of cooked food in pre-annexation days, owing to constant danger of raids, he includes . . .: *Vainiim kan.*—"As the name implies, this is roasted maize, and it is prepared in exactly the same way as *Vai kan.* Occasionally, when it is to be eaten the same day, bananas are pounded into the grain as a change of flavour."

He describes the *Vai kan* just referred to as follows:

The name means roasted millet, *faang klawr* again being the variety used. The grain is soaked in water for a minute or two to damp it thoroughly and is then steamed as if to prepare it for fermenting, after which it is spread on mats to dry in the sun. In the final stages of preparation the swollen grain is roasted in a *peibung* until it bursts like puffed wheat. The whole is then pounded with salt or honey and made into convenient lumps which are taken on hunting parties, etc. *Vai kan* is regarded as best of all foods for "sticking to the ribs" but it is very dry, especially the salted variety, and for this reason is not used during hot weather in areas where water is scarce . . . . . .The *peibung* is the traditional grain-roasted pot, shaped rather like a beer-pot, but with a large hole in one side. Its very existence proves the antiquity of the roasting method of cooking.

The same authority lists under the heading "Daily food in the home":

Thiah Var:
This is the commonest food of the present day, and it is generally made with maize, millet being reserved for beer-preparation or the travel ration. The maize is pounded to break the grains and then sieved and boiled in water. It is eaten with any sauce that is going, after the liquid has been drained off. When consumed as a broth with the water in which it is cooked it is called *ti sawp,* and if pumpkin and other leaves are added as a flavoring it becomes *buh ber.*

The harvest is apparently later than in most of the Assam Hills, presumably for climatic reasons. Stevenson states (l.c., p. 41):

No sooner is the millet crop safely gathered than the maize ripens in August and September. In harvesting maize also the Chin use no knife but tear the cobs off by hand, removing the outer cover and turning the inner ones back to act as ties when the cobs are eventually stored under the rafters of the house.

With regard to the use of maize for beer-making, Stevenson records (l.c., p. 113):

In the Central Chin Hills there are three recognized types of beer: *zu ha,* made from first-quality cleaned millet; *zu pi,* made of husked millet mixed with its chaff; and *vainiim zu,* made from Maize . . . . . . [*vainiim zu*] is made of pounded Maize, which after being soaked for a day to soften is treated like the millet used for *zu ha.* Like *zu ha,* it will not keep for long and is therefore prepared shortly before use. This *zu* being the cheapest, is most often used in the home on day-to-day occasions.

Maize seems to be too important for human consumption to be given directly to domestic animals. Stevenson notes, however (p. 114): "Incidentally, fermentation of grain for beer does not waste the solid residue: this by-product is added to the pig-food and gives strength and substance to the unappetizing bulk of banana stalk which is the other main ingredient." As a corollary to this, I may add that this use of the fermented grain of millet, rice, maize, etc., for feeding pigs is a

universal practice among all the Nagas and other tribes.

The Chin word for Maize is *Vainiim*.

13. THE KUKIS:—

The Kukis live in the Southern Naga Hills, and in Manipur State. I have once visited a few Kuki villages in the former area, among whom maize was grown and used in precisely the same manner as among their Naga neighbors: as a catch-crop for consumption while fresh, for popcorn, and to a small extent for beer-making. The same types are grown. The name for Maize among the Thadou branch of the tribe is *Kolbu*, which is said to mean "Burma Food": an interesting point since the Thadou Kukis are generally regarded as having close kinship with Northern Burma.

14. THE MIKIRS:—

The Mikir tribes have been very little studied. Their system of shifting cultivation is very primitive. Maize is among their subsidiary crops. I have been told by a member of the tribe that the large-grained types are most grown, but the small types are also used. The Mikir word for maize is *Thengthe*. I have not been into the Mikir Hills.

15. THE KHASIS:—

Varieties grown: The Khasis have for generations been in close contact with the British, Nepalese and Indians, and Asiatic, African and American varieties have been introduced and are by now inextricably mixed with older types. Most of the tribe cultivates at over 4,000 feet, and it is doubtful if the small-grained types were ever used to any extent.

Ecology and technique: As a mixed crop, together with rice, millet and Job's-tears. Nowadays the Khasis have a large-scale potato-growing industry, and maize is often grown in the potato plots, interspersed between the rows of potatoes. It is also grown as a pure crop.

Uses: The original uses were for food, mainly as a catch-crop, the ears being eaten boiled or roasted. Some is put aside for popcorn, and in parts of the area it is prepared by placing the grain, with some sand, in the cooking-pot, and heating it over a fire. Maize is become a fairly important cash crop for sale in the bazaar at Shillong. It is used to some extent as pig food.

Storage: Very little is stored, except for seed. The ripe ears are hung up in the house.

Traditions, folklore, etc.: The Khasis state that maize is among their ancient crops. The word for it is *Riew Hadem*, meaning "Grain of the Hadem People." The Hadems are a small branch of the Kuki tribes who live in close contact with the Khasis in the extreme southeast of their area.

16. THE GAROS:—

Varieties grown: G1–G5.

Ecology and technique: The seed is dibbled in lines among the rice and other crops in the *jhum* fields. It is sown about March in most parts and harvested in

June. In some of the warmer areas it is often planted earlier, and I have seen plants with the ear already formed in April.

Uses: Although the staple crop of the Garos is rice, they are hard-pressed for land and food is often short. Maize is an important catch-crop, and is almost entirely used as it ripens. The fresh ears are either boiled or roasted. Very little is stored, and this stored grain is pounded and eaten boiled, either alone or with rice. The smallest variety grown is used only for popcorn, and is prepared by heating it in a cooking-pot with a little sand. Maize is too precious for human consumption ever to be used as pig food; and is said not to be used for beer, which is made entirely from rice.

Storage: When stored for winter use, it is stripped from the ear and put in round baskets. Stock for seed is hung up in the dwelling-house.

Traditions, folklore, etc.: The Garos say they have always grown maize, and got it with their main crops "out of the ground."

* * *

All the foregoing tribes live south of the Brahamaputra, which has always been an effective, but by no means absolute, barrier to contacts of culture. The notes which follow describe the cultivation and uses of maize among the tribes of the outer Himalayas, within the political boundaries of Assam.

17. THE DAFLAS:—

Varieties grown: Serial Nos. 1–4.

Ecology and technique: Maize is grown as a mixed crop along with rice and millets, under the same system as among the Naga tribes. It is the earliest crop sown, and is often dibbled in before the rice, the usual month being March, although I have seen fields sown in February.

Uses: Rice is the staple food among this large tribe, but their technique of shifting cultivation is slovenly and haphazard, and probably for this reason, subsidiary cereal crops of millet and maize are of considerable importance to supplement the rice supply. Maize is both grown more than among the Naga tribes, and much more, perhaps most of the crop, is stored for winter use. I have not been to the Dafla country while the maize was ripening, and cannot say to what extent it is eaten fresh and functions as a catch-crop. However, in normal seasons, it is a subsidiary crop to help out the rice in the winter rather than a catch-crop for immediate use. In the summer following a poor harvest, the people would, of course, be forced to use their maize as soon as it was developed enough to eat. The main use of the stored maize is for food, since the grain is more easily broken up and mixed with rice. For this reason, the smaller-grained of the main types is preferred since the grain is more easily broken up by the pestle-and-mortar grain-pounders. Sometimes it is crudely milled between flat stones. A proportion of the maize is mixed with millet (Eastern Daflas) or with rice (Western Daflas) for beer-making. In good seasons it is used for pig food. Even the dried ears are

often roasted and eaten off the cob.   I have several times seen them given to children as "snacks" between meals.   All types are used for popcorn.   For some years past, Daflas living fairly near the Plains of Assam have carried on a small trade in maize with tea-garden coolies.   The Daflas grow only the larger-grained types, and have far fewer types, partially accounted for by the different status of the crop since the large-grained types are clearly more economical for storage than are the small-grained.   Climatic factors may, however, enter into it, and it is also perfectly possible that the Daflas have never had the smaller types as grown on the Assam-Burma border.

Storage: Maize is stored in the granary along with other grains.   Among the eastern (and more primitive) section of the tribe it is kept on the cob, and the ears are heaped up in a roughly-made rectangular bin in one corner.   The western Daflas strip the grain from the cob and store it in large round baskets, usually with the cobs wedged over the top as a protection against rats.

Traditions, folklore, etc.: I have several times questioned Daflas on this.   They simply state that they have always grown maize.   The Dafla word for maize is *Topothe.*   The smaller type grown (Serial 4) is known as *Nyamatup.*

18. THE ABOR TRIBES:—

I have only visited the Padam and Minyong Abors.   The other main tribe are the Galong Abors, whose country is adjacent to the Daflas and who are probably very closely related to them.   The following note deals only with the Minyong and Padam Tribes.

Varieties grown: Nos. 1–4 (of first consignment).

Ecology and technique: The Abors grow their maize as do all other shifting cultivators as a mixed crop among their rice and millet.   They are, however, unique in that they practice double cropping.   The first crop is sown during the month of February and is harvested in June.   As soon as it is ripe, a second sowing is made in the same field, and is harvested in October.

Uses: The first crop of maize is used purely as a catch-crop, and is eaten while the ears are soft, either boiled or roasted.   The second crop is left standing until the ears are thoroughly ripe and the grain hardened off.   It is then stored and used during the winter either as a food or for making beer.   The proportion that goes for beer-making or for food is said to vary with the economic position of the household and the general abundance of the crops in any one year.   In general, maize is an important crop, although rice, Job's-tears, and millet are the staple foods.   It is used to some extent for pig feed.   Popcorn is also made, but not to any extent.

Methods of Storage: The grain from the second sowing is stored, stripped from the ear, in round baskets in the granary.

Folklore, traditions, etc.: The Abor tribes simply state that they have always had maize among their crops.   Their folklore credits them with having obtained

all the main crops "On the horns of the tame Bison," and I have been told specifi-cally that maize is included. The name among the Minyong and Padam sections of the tribe is *Sepa*. The main type used (a large golden or red flint maize) is called *Pade-Pasing Sepa*.

19. AKA TRIBE:—

I have not visited this small tribe, but I have met and talked with several mem-bers of it. They all told me that their most important crop is maize, which is grown in their fields along with dry rice. According to my informants, the Aka tribe originated in the Assam Valley, whence they were driven up into the hills many generations ago. At that time their main (or only) crop was rice, and they learned to use maize from the Monba tribe immediately to their west. They in-formed me that they grow the same varieties as the Monba tribe. The average altitude of cultivation in the Aka Hills is of the order of 5,000 feet.

20. MONBA TRIBE:—

Varieties grown:

1. *Phentang*. Serial Nos. 1 & 2 of first consignment.
2. *Num Phentang*. Serial No. M1.
3. *Khana Phentang*.

The first two are indigenous: the *Khana* is a South African dentate maize intro-duced a few years back by the government. *Khana* means tooth.

Ecology and technique: The Monbas differ from all other tribes of the Assam Hills in that they are a civilized people whose whole culture and social organization is of Tibet. They have a well-developed system of farming on permanent fields. Their maize is grown as a pure crop in rotation with other cereals and in the permanent fields. It is sown in May and June, and is harvested from late September to early November. The lateness of the sowing as compared with other areas is due to the need of fitting it in with their system of rotation. Sowing is entirely by broadcasting, and the ears are pulled off by hand. The variety *Phentang* is the most grown, and is in large fields. The variety *Num Phentang* is grown in small amounts, and is relegated to odd corners, edges of fields and to the few areas of shifting cultivation. The introduced dentate maize, *Khana Phentang,* is almost entirely relegated to the areas of shifting cultivation. The reason for the different technique will be clarified below.

Uses: The Monbas, with their advanced economy, grow a variety of grain crops, all of some importance. These include maize, barley, rice, buckwheat, millets, *Chenopodium*, cockscomb. However, with the exception of a few villages at 9,000 feet and above, the most important crop is maize, which is said to be more important than the others put together, and is the staple food. The main uses of the grain are:

1. For the ordinary food, the variety *Phentang* is ground to a coarse flour by

means of the ordinary Tibetan water mill. The flour is usually boiled. This flour is known as *Phentang bukpu*.

2. A small proportion of the same variety is eaten when the ears are still soft.

3. The *Phentang* is slightly roasted and then flattened and partially broken up by light pounding. In this form it is chewed as a relish, especially while liquor is being drunk, and plates of it are always offered to visitors. The local name is *kakung*. A great deal is consumed in this way, and the *kakung* is also an article of trade in Tibet.

4. The *Phentang* is used to a fair extent in brewing of beer and distillation of a weak spirit. This is said to be the use of the introduced variety *Khana Phentang*.

5. For popcorn, the variety *Num Phentang* only is used, and it is grown for that purpose only. It is popped by heating in an earthenware vessel with a little sand.

As far as I know, virtually all the maize crop is used for human consumption only, except that the "leavings" from manufacture of liquor go to the pigs. By far the most important type is thus the *Phentang*, a strong-growing, large-grained golden-yellow or occasionally red, flint type.

Methods of Storage: This aspect is also interesting. When the maize is ripe, the ears are left for some weeks on the plant to dry. They are then gathered, and the enclosing leaves removed. The ears are then stacked on the fields in solid rectangular panels up to 20 feet long, by 10 feet high, and perhaps 2 feet thick, the structure being raised off the ground by a slight framework of sticks. The panels are often L-shaped. A field, when the crop is stacked, is a beautiful sight dotted with these solid patches of golden yellow, the more so since the few scarlet ears are suspended over the top for color effect[1]. The crop is left thus for a month or less to dry off thoroughly, after which the ears are carried home to the village, and the grain removed either by hand or threshing with a short stick. It is stored in large round baskets in the upper room of the two-storied house. The seed for next season is left on the ear and hung up on the rafters.

Traditions, folklore, etc.: The Monbas simply state that they have always grown maize, and that as far as their traditions go back it has been the staple food crop. On the other hand, they have a well-established tradition that they first got their rice from the Plains of Assam. By religion they are Buddhists (every other tribe in the Assam Hills is Animist), and it is both interesting and significant that the first ears of maize to be gathered are placed in the village temple as an offering, while they deny any such practice in the case of their barley which (together with their Buddhism) they must have obtained from Tibet. It is also a common sight to see a few ears of maize hung up as offerings inside the temple, or placed on small wayside shrines. I have asked members of the tribe if they have any special rites, dances or festivals for their maize, and in all instances this was denied. I would

---

[1] It is possible that the original purpose of suspending the red ears was to ward off evil spirits from the fields.

not, however, like to state categorically that my informants were accurate. In dealings with tribal peoples knowledge of religious custom can only be got by long and close acquaintance or direct observation.

21. THE APA TANI TRIBE:—

Varieties grown: Serial Nos. 1–4 of first consignment (as for Dafla Tribe).

Ecology and technique: The Apa Tanis, although a primitive people without writing, etc., have a very highly developed system of irrigated rice cultivation for their staple food supply, and practice shifting cultivation extremely little, if at all. The maize is grown in small quantities in little garden plots in and around the village. The tribe inhabits a small area in the Dafla Hills and the varieties grown are the same.

Uses: Maize is not an important crop. A proportion of it is eaten soft on the ear. Some is stored, and is prepared by first roasting it in a clay pot and then pounding it to a coarse flour. It is said to be eaten mainly by old people with decayed teeth, but this needs checking. Popcorn is prepared in considerable amounts, and is made by putting the grain into the glowing embers of the fire, and picking it out with bamboo tongs as it bursts. I am not sure if the other method of heating the grain in an earthenware pot is used.

Methods of Storage: The small quantity stored is kept with the rice in separate granaries.

Traditions, folklore, etc.: I have no information.

22. THE MISHMI TRIBE:—

I have once visited a small section of this very primitive tribe, and have only the scantiest information. Their shifting cultivation is rough and ready. Maize is included among the crops and Mishmis have told me that it is of moderate importance. I have seen Mishmi women making popcorn by putting the grain in the edge of the house fire, and picking it out as it bursts.

MAIZE IN HILL AREAS OUTSIDE THE BOUNDARY OF ASSAM

BHUTAN:—

I have talked to many traders and others from Bhutan and am told by them that maize is grown everywhere, and is a fairly important crop. A large yellow type is said to be the most widely grown, and is presumably the same as the *Phentang* of the Monba tribe on the Assam-Bhutan border.

SIKKIM:—

As for Bhutan. Writing a hundred years ago, Sir Joseph Hooker ("Himalayan Journals," Vol. II, p. 78, footnote) states that he was given popcorn in North Sikkim. He describes it as, "Called pop-corn in America, and prepared by roasting the maize in an iron vessel, when it splits and turns partly inside out, exposing a snow-white spongy mass of farina. It looks very handsome, and would make a beautiful dish for dessert." Hooker also records (Volume I, p. 157) seeing, in May, 1848, the maize just sprouting in North Sikkim. He goes on to record the

curious statement that "This plant is occasionally hermaphrodite in Sikkim, the flowers forming a large drooping panicle and ripening small grains: it is, however, a rare occurrence, and the specimens are highly valued by the people." Unfortunately, he does not tell us if he actually saw such plants, or if he was recording from hearsay.

Maize is among the crops of the small Lepcha tribe of Sikkim. In his book "Himalayan Village" (published in 1938) Mr. G. Gorer refers several times to maize cultivation. He notes (p. 95) that wheat and maize are used for food when rice is short, but states that "they are not liked." He notes that the maize is sown in March (p. 94). This is confirmed by Major J. Morris in his book "Living with the Lepchas" (1938, Chapter 9) where he several times refers to maize as being among the crops raised by this tribe.

NEPAL:—

Of this region, I have the scantiest information. Nepalese immigrants into Assam have told me that they grow considerable quantities of maize in their own country. Maize is an invariable crop of these immigrants, even when they settle in the hot plains of the Brahamaputra Valley. They grow large yellow or white forms, the same or very similar to the main type of the tribes of the Assam Himalayas (Abors, Daflas, Monbas).

BURMA:—

Unfortunately, I have been able to get no information concerning the Shans, Wa's, Karens, or any of the hill peoples in Burma except the Chins as recorded above. Of the large Kachin tribe, who live in the extreme north of the country and whose hills are contiguous to the Mishmi Hills of Assam, Mr. J. L. Leyden has recorded (introduction to a pamphlet "The Kachins of the Hukawng Valley" by Kawlu Ma Mawng, 1944, p. ix):

> The Kachins are rice eaters, and their agriculture is mainly concerned with the production of their staple food. Kachin agriculture is chiefly concerned in the extremely wasteful and inefficient shifting cultivation . . . . . . As the cultivation and sowing is crudely carried out the Kachins invariably find themselves with a poor crop of rice and are compelled to work subsidiary crops of maize, millet and yams to avoid starvation.

While this somewhat bald statement as to why maize and millet are grown can hardly be accepted at its face value, especially *vis a vis* the tribes of Assam, it at least indicates that maize is an established subsidiary crop, probably in very much the same way as among the Naga tribes.

MANIPUR STATE:—

The Naga and Kuki tribes of Manipur State are of the same stock as those of the southern Naga Hills (see above under Cachar Nagas and Kukis), and it is reasonably certain that they grow the same maize and in the same way as do their neighbors. The Manipuris proper inhabit the highly irrigated plain of the Manipur Valley. I have no information as to whether they grow maize, but consider it unlikely that it is of any importance as their fields give them a considerable surplus of rice.

HISTORY IN THE ASSAM HILLS

As we have seen, maize is grown by all the multifarious peoples of the region. This wide distribution does not in itself mean that it is of necessity an ancient crop. Once introduced and given favorable conditions for its spread, any crop can spread with rapidity, even in remote areas during a very few generations. This has taken place in the Assam Hills, a good instance being the potato. Another such crop is manioc, which is now grown in at least three widely separated ranges of hills. But both these crops are universally recognized as being introduced after the coming of the British. In the Garo Hills I was told by illiterate villagers that manioc has been grown by them for about twenty-five years; and in the northern Naga Hills it is said to have been with them for two or three generations. But in the case of maize I was simply told by every tribe that they have always had it among their crops, and any suggestion that it came from outside was ridiculed. An exception to this, as recorded above, is the Aka tribe, a small tribe of the Assam Himalayas, who believe their maize to have been obtained from neighboring tribes many generations back. I have constantly inquired in tribal villages, and particularly among the old men of the community, as to when and how they first got their main crops. The reply was always the same in regard to millets, taro, maize, Job's-tears, and yams. They have always been grown, and no one can say when or how they were first obtained. In some cases this is true with rice, now the staple crop among the majority, but there are indications that rice is a more recent food than the rest, although it is undoubtedly a very ancient crop and has been grown in Asia for some thousands of years. Thus, among the Chang, Yimchungrr, and some of the Konyak Nagas, the people even now depend on roots and cereals other than rice for their food supply and state quite openly that they are older crops, maize not excluded. The same is true of the Monbas, who have a definite tradition that maize has "always" been their main crop, while rice was obtained many generations ago from the Plains of Assam.

Furthermore, in the case of rice there are established legends to account for its origin. They have been recorded for the Naga Tribes by Professor Hutton and Mr. Mills (in the series of monographs on the Naga Tribes), and for the Lakhers by Mr. Parry ("The Lakhers," 1928), while I myself have been told folk tales by the Daflas, Minyong, Abors, and Khasis. But there is no legend known to account for the origin of the other cereals, millet, maize, and Job's-tears, the inference being that rice is more recent while the others are lost in the mists of antiquity.

The existence of a distinct name for maize is everywhere indicative of a respectable age, the more so when we note that in several cases where a variety has been introduced by the British or by Nepali immigrants, the fact is well-known. Among a few tribes, notably the Khasis and the Lhota Nagas, the tribal name is indicative of origin from neighboring peoples. This is not, however, quite conclusive, as the generalized name could be based on a variety got from the tribe in question and which supplanted older and more indigenous types.

My notes on the religious aspect are particularly scanty. However, the dance of the Lakhers, the use of maize in funeral rites among the Lushais in deliberate preference to rice, its importance as a votive offering among the Monbas, the part it plays among the agricultural ritual of the Rengma Nagas, and the existence of a special tutelary deity among the Chang Nagas, all point to its being a well-established crop, the more so since primitive peoples with animistic religion are invariably shy of incorporating new crops into their agricultural ritual.

The wide distribution, the positive statements of the peoples themselves, the position relative to the crop complex, the existence of distinctive tribal names, and the place in religion, all point to a long history, going back for centuries at least, for maize among the hill tribes of this region. As we shall consider immediately, this is fully supported by the general economics of the crop and the variety of uses to which it is put.

GENERAL ECONOMICS

This is a major study in itself, and the factors involved are many. Among them may be listed: (1) climate; (2) the varieties available; (3) techniques of cultivation; (4) other crops grown; (5) uses for which the crop is grown.

Taking first the climatic factors, the *climate* of the Assam Hill areas varies from sub-tropical to sub-temperate, and maize is grown at all elevations from a few hundred feet to 6,000 feet. In general, it is of more importance to the tribes living at high altitudes, a state of affairs not unconnected with absence of rice varieties suitable for cold elevations, as among the Chang Nagas and surrounding tribes, and possibly among the eastern branch of the Lushais and the Chins.

Varieties grown in any one area or by any one tribe are clearly dependent, within the limits of the climate, on the culture contacts, the purpose for which maize is needed, and so on. There is a far greater variety of types grown along the Assam-Burma border (Nagas, Lushais, and Chins) than in the outer Himalayas (Abors, Daflas, Monbas), although maize is on the whole more important in the Himalayan region. Since all tribes of the Himalayas store part of their maize, inspection of granaries after the crops had been harvested have enabled me to survey with reasonable accuracy the varieties grown, and the peoples of this region seem to cultivate only the larger coarser types, the small several-eared forms being entirely absent and apparently confined to the Assam-Burma border. These very distinctive small varieties are moreover grown at low altitudes, and I do not think them to be cultivated at elevations higher than 4,000 feet, so that they are all associated with the sub-tropical rather than the sub-temperate zones.

Although the climatic conditions of the inhabited parts of the Himalayas are, on the whole, colder than in the other hill areas with which we are concerned, there are thickly populated areas in the low sub-tropical foothills of the Abor country which are very similar to the outer Naga Hills; and the inference is that the tribes of the Himalayan region have never had these small maizes. This seems to link up

with the larger number of tribal groups in the Burma region and the greater frequency of migration to and from the area, as well as local movements within these particular hills, each group contributing its quota to the complex of crops over the passage of time and passing them on by local diffusion.   Leaving aside any possibility of a variety having originated at some remote period in the area where it is now grown, each tribe seems to have accumulated its types of maize by culture contact.

For reasons given I do not consider that there has been any great production of varieties by hybridization.   In the data recorded above some support is given to this origin of varieties within a tribe.   Thus the Lushais regard a proportion of their maize varieties as their own, one as obtained from their Chin neighbors, and two as of recent introduction from the Nepalese and the British.   The Lhota Nagas of the hotter foothills have three varieties they regard as indigenous, or at least of very ancient introduction, one obtained from the Angami Nagas, one from the Ao Nagas, and one from the Nepalese.   It is stressed that the word "indigenous" implies only that a variety has been grown for a period for its ultimate origin to have been forgotten in the traditional memory of the tribe, and in no case necessarily means that it originated with them.

Technique of cultivation:—As indicated already, in the majority of cases the maize is grown in lines, small patches, or single plants among the other cereal crops.   Only among the Monbas with their advanced farming, the Angami Nagas and the Apa Tanis with their system of irrigated rice growing, and perhaps among the Lushais, the Chins, and Akas, is it normally a pure crop.   At first sight, this rather haphazard technique seems conducive to hybridization, particularly where five or six types are grown by a single village.   But examination of granaries shows but a small proportion of parti-colored ears.   The reasons are not far to seek.   In the first place, there is a general prejudice which I have often heard expressed against saving seed from any plants which do not look pure bred; secondly, as I have demonstrated by experiment, different types flower at long enough intervals apart to act as a fairly effective check on cross-pollination; thirdly, all types are not extensive, but in every area I have visited, a walk through the fields shows different types grown in different stretches of land and certain types are definitely looked on as more suited to distinct soils and elevations . In clarification of this, it is important to remember that a village community cultivating on hill slopes will almost invariably have in use at any one time fields varying up to several hundred feet in height above sea-level, with corresponding diversity of exposure to winds, etc.   It therefore stands to reason that where different varieties of any crop are grown they will be dispersed according to individual suitability to local variations in climate and soil conditions.   As a general rule I have seen the larger-grained types of maize relegated to the higher-altitude fields, while the small popcorns and several-eared forms are sown on the lower, warmer slopes.   Finally, the tribes are perfectly well aware that sowing different varieties mixed together leads to the

hybridization they are anxious to avoid, and for obvious reasons deliberate segregation is practiced.

Uses to which maize is put: Within the limits of the climate and the varieties available, the purpose for which maize is grown is naturally the determining influence of every aspect of a crop, maize as much as any other. As the whole background of the economics, is the major fact that in the Assam Hills *rice* is the cereal crop preferred above all others, and wherever it can be grown and suitable types are available it is now the staple cereal. In qualification of this, we have already referred to maize as being the main grain crop among the Monba tribe of the Assam-Bhutan border. Members of the tribe have, however, told me that they prefer rice when they can get it, but since their arable land is limited and there is very little fit for irrigation, it is more economical to grow maize as a main crop. In a somewhat similar way, among the Chang Nagas and neighboring smaller Naga tribes, millets, maize, and Job's Tears are the most important cereal crops largely because the people have no rice varieties suitable for the cold altitude of their lands. Within the past two or three years the Chang tribe has made requests to the government to help obtain seeds of rice suitable for this cold climate. I do not know if this applies among the eastern Lushais and the Chins, but the inference is that it does, since the Lushais dwelling in warmer parts of the hills are all rice cultivators. The detailed uses of maize as outlined above are:

1. A catch-crop, eaten while the grain is soft. (All tribes.)
2. Stored for food in the winter, either as a reserve secondary to rice, or more occasionally as a main crop.
3. For beer-making.
4. For popcorn.
5. For pig food.
6. As an article of trade outside the village.

The first named is the most universal use of the crop, and applies to all tribes. For eating fresh, as a catch-crop, the smaller, several-eared types (other than the popcorn) are often preferred by those who grow them. This is apparently due to their soft, sugary grains which are appreciated both in themselves and as an alternative to the harder less sweet types. I think this to be the main reason for survival of these small types, since the grain is not nearly so economical for storing as winter-food as are the larger, "coarser" forms, and I know of no tribe which stores the smaller varieties for any purpose other than popcorn and perhaps for beer *(vide infra)* to a very limited extent. A point of some importance in connection with the use of maize as a catch-crop and for immediate consumption is the fact that different types grown in the area in question differ very appreciably in the time taken to mature, the small several-eared forms being several weeks slower than the larger types. It is of course well known to the peoples who grow them, and who naturally therefore space out the crop on this basis, to cover as long a period as is necessary.

The dried, ripened grain stored for the winter is, as we have seen, of primary importance among the Monbas, Changs and neighboring tribes, the Chins, and Eastern Lushais. It is of secondary importance among the Daflas and the Abor tribes, and the Sema Nagas, and is of fairly minor importance among the rest. It is, however, essential to maintain a balanced perspective and to remember that while statements of this kind are accurate in general terms, the whole balance of crops and their use is naturally fluid, especially among a primitive tribe with a comparatively unstable economy, and any general picture is only true for the actual time a survey is made. Thus, local conquests of tribe by tribe were taking place in the Naga Hills and elsewhere before British Administration was introduced, conquests which were accompanied by varying degrees of change in the pattern of culture, the crops not excluded. Nor has change ceased since more settled administration was started. In most hill areas of Assam, the government has constantly been trying to persuade tribal peoples to change over from shifting technique for mixed crops to permanent irrigated cultivation for rice.

Similarly, in a more restricted sense still, a season of poor rice harvest in the autumn means that the supplies for the winter and following spring will soon be exhausted, and under these conditions a people such as the Daflas who normally consume a proportion of their maize as it ripens and store a proportion for beer and a reserve of food during the winter, will naturally use a greater amount for food and less for liquor, and *vice-versa*, after a good harvest, when there will probably be even a little to spare for the pigs. To narrow this down even further, from the tribe or the village to the individual household among peoples for whom rice is the most important of many crops, the subsidiary crops of maize, millets, and roots are naturally most important for the poorer people of the community whose rice supply runs out before the end of the season and the start of the next year's main harvest, and who live rather from "hand to mouth" depending to a greater or lesser extent on the "catch-crops" for their main food supply.

The use of maize for beer is governed by the same factors as for food. Among most tribes rice is preferred for beer-making. Possible exceptions to this are the Sema Nagas, who seem to use maize from choice, and the Eastern Daflas, who grow considerable quantities of millet solely for beer. It follows as a natural sequence that the worse the food crops in any one season, the less will be spared for beer and the more will be needed for human consumption. Very often beer is made from a blend of a variety of ingredients, the technique varying even from village to village within the same tribe, and maize will normally be included in the list of grains used for the brew. Thus, among the Chang Nagas I have been told that beer is made by mixing maize, Job's-tears, millets, and *Chenopodium* in fairly definite proportions. I have not been able to discover that any maize variety is used or grown specifically for beer, but this is a point calling for more detailed investigation.

Popcorn is used everywhere, and special varieties are normally grown for this purpose only. The popcorn is made either by roasting the grain in a pot, often mixed with a little sand, or by simply placing the grains at the edge of the fire and picking out the popped grains with bamboo tongs as they burst.

The above notes deal with maize among the tribal peoples of the Assam Hills, and the plains areas of the Brahamaputra Valley and the southeast of Assam and Pakistan have not been considered since maize is not grown there by the indigenous population. It is, however, possible to grow it in the plains, and it is a common crop among Nepali immigrants. It is therefore perfectly feasible that it was grown in past epochs by the aboriginal population of the Assam Plains who might well have abandoned it with the development of a highly organized system of irrigated cultivation for rice.

Part II

EDGAR ANDERSON

The data reported in this paper are basically simple, being essentially a morphological survey of the varieties of maize grown by the Naga. However, the accurate assembling of these critical data required the cooperation of a number of individuals and institutions. The varieties collected by Stonor were numbered by him, and selections from most of them were grown in his experimental plot in Shillong, Assam. Herbarium specimens of the tassels and photographs of several of the more outstanding varieties were then forwarded to the Missouri Botanical Garden. Samples of the original ears collected by Stonor were sent to the Royal Botanic Garden at Kew where they were photographed. The ears were then shelled and the seeds, identified by their original numbers, were sent to the United States, where they were fumigated and forwarded to the Missouri Botanical Garden. The empty cobs were imported separately and were sterilized by heat before being released. These extraordinary precautions were necessary because two of the worst diseases of maize are found in southeastern Asia. At the Missouri Botanical Garden samples of the seeds were germinated and the seedling characters were studied. Several representative cobs were turned over to Dr. L. W. Lenz for histological examination and were included in his recent (1948) survey. Early the following spring the seeds were forwarded to Dr. E. G. Anderson of the California Institute of Technology where they were planted in the maize-breeding plot at Arcadia, California, one of the most favorable sites in this country for tropical maize. With the cooperation of Dr. A. E. Longley of the U. S. Department of Agriculture and Dr. William L. Brown of the Pioneer Hi-Bred Corn Company, material for cytological examination was obtained from many of the cultures and chromosome knob numbers and knob positions were determined from pachytene smears. During the growing season I worked at Arcadia for ten weeks where all the cultures, aside from a few late-maturing varieties, were scored for plant color, representative plants

were photographed to scale, herbarium specimens were made of tassels, internode diagrams were made of mature plants, and the details of tassel and ear morphology were recorded.   Eventually all the data and materials were assembled at the Missouri Botanical Garden—the herbarium specimens and photographs from Shillong, the photographs and shelled cobs from Kew, the photographs, herbarium specimens, and notes from California, the knob counts made by Dr. Brown and myself, and the histological information from Dr. Lenz.   We are also indebted to Dr. Herschel Roman and Mr. Earl Patterson for internode measurements and specimens of varieties which matured after I left California.

The following collections were grown; the information concerning each variety was supplied by Mr. Stonor:

SERIAL No.	LOCALITY	TRIBE	REMARKS
1	E. Dafla Outer Himalaya	E. Dafla	Sown Feb.–March; ripe June. Much grown at 3000 ft. Local name *Topothe*. Number of ears 2–4.
5	N. Cachar Hills	Kuki	Grown at 2000–3000 ft. Number of ears 4–5.
6	N. Cachar Hills	Kuki	As for 5, with which it is grown.
7	N. Cachar Hills	Zemi Naga	Grown at 1500–4000 ft. No precise details. Said to give 2–3 ears. Sown about March.
8	N. Cachar Hills	Zemi Naga	Grown at 2000–3000 ft. Said to be slow-ripening. Gives 4–6 ears. Sown about March.
9	Naga Hills	Angami Naga	Grown at 3000 ft. Details as for 8.
10	Naga Hills	Angami Naga	Grown at 3000–4000 ft. No other details.
11	Naga Hills	Angami Naga	Grown at 3000–4500 ft. No other details.
12	Naga Hills	Ao Naga	Grown at 3000–4000 ft. Sown Feb. to March; ripe June–Sept. Said to bear 7–8 ears. Local name *Lozar*.
13	Naga Hills	Ao Naga	Grown at 3000–4000 ft. Sown late March; ripe June–July. Has 3 ears. Said to be very sweet. Local name: *Mapok Memdi*.
14	Naga Hills	Sema Nega	Grown at 3000 ft. Sown March to April; ripe June to July. Has 3–4 ears. Local name: *Azheu*.
15	Naga Hills	Sema Nega	Grown at 2000–3000 ft. Sown March–April; ripe June–July. Said to have 6 ears. Local name *Azehuge*.
16	Naga Hills	Sema Nega	Grown at 2000–3000 ft. Sown March; harvested July. Said to be sweet. Has 2–3 ears. Local name *Mesheu*.
17	Naga Hills	Sema Nega	Grown at 3000 ft. Sown March–April; ripe June–July. Has 2–3 ears. Local name *Kolami*.
18	Naga Hills	Sema Nega	Grown at 2000–3000 ft. Sown Feb.–May; ripe May to Sept. Has 6–7 ears (verbal report). Local name *Anila*.

In addition, seven varieties collected in the Lushai Hills were grown. Since they were in general very similar to the above and included no peculiarities not represented in the Naga collection, no detailed account of them has been prepared.

General Appearance:—

As compared with most collections of native varieties from South and Central America, one of the most outstanding characteristics of these Assamese varieties was the uniformity of several of the varieties and their differences from each other. This bears out Mr. Stonor's remarks as to the skill and determination of the Naga in keeping their varieties pure. Several of the cultures, though grown directly from seeds collected among the Naga, were as uniform as a good inbred line. It is probably significant that those varieties which were most unlike anything previously known in our studies of exotic maize were the most uniform, while the one variety most closely resembling the maize of Latin America was among the most variable (see below under "Caribbean"). The conspicuous differences between certain of the varieties make it difficult to generalize about them as a group; nevertheless there were certain definite trends which characterized the entire collection. Almost without exception these trends were most strongly marked in those kinds which morphologically were the most extreme such as "Late Upright" and "Late Sidewise."

Fig. 1. Internode diagram of one plant of Stonor 18 ("Late Sidewise"), grown at Arcadia, Cal. Circles represent tassels, elliptical figures ears. The diagram is as if the stalk were cut at the nodes and the dissected internodes were laid side by side in succession, the lowest at the left, the uppermost at the right, and then a line (the line seen in the diagram) were drawn connecting their summits. The scale at the left (in centimeters) indicates the lengths of the internodes. It will be noted that there were over 30 nodes on the plant, none of which was over 8 cm. long; that there 4 ears; and only 4 short internodes between the upper ear and the tassel. Small lines at the left of the diagram indicate nodes at which there were well-developed prop-roots.

Figure 1 shows a drawing to scale of a typical seedling. The short, narrow tap-root, the numerous adventitious roots from the mesocotyl, and the broad mesocotyl and coleoptile are characteristic.

One of the most unexpected characteristics of these varieties was their green color. Not only were they mostly without the bright plant, tassel, and silk colors of so many Latin American varieties, but some of them had no visible anthocyanin pigment in any part of the plant. The group as a whole had a strong tendency to green silks, green anthers, green leaves, and green culms. There was also a strong tendency for the leaves to have a more evenly green appearance, like certain varie-

ties of *Sorghum*. In nearly all the maize of the New World there are minute differences in the intensity of the green above and between the veins, giving the leaves macroscopically a kind of longitudinal grain. The Assamese varieties tended to be evenly green throughout like a green plastic dish.

The collections among the Naga were outstanding in their lack of vigor, and this was quite as true in Shillong, Assam, as in Arcadia, California. Some were mid-season, others late or very late, but all of them developed slowly. From the time the tassel made its first appearance until it was completely out of the leaves and shedding pollen, as much as four weeks might elapse. One of the most outstanding characteristics of the maize of the New World is its vigor. Nearly all maize varieties grow and develop rapidly; the controlled heterosis of hybrid maize is merely an extreme standardized example of a tendency nearly universal in the New World. This vigor was absent in the Assamese varieties. Whether midseason or late in their maturity they poked along from week to week. The internodes were short; in the most extreme variety none of them was over 10 cm. in most plants. Nor was this the result of their having been transplanted from Assam to California, since the samples grown by Stonor in Shillong exhibited these same characteristics.

The internode patterns were highly peculiar. In addition to short internodes, the varieties from the Naga tended to have many ears (as many as four or five in some varieties), and the internodes above the ears were so short and crowded that the silks of the uppermost ear were sometimes tangled in among the lower branches of the tassel (see plate 22). Not only were the upper leaves crowded together but as Collins noted (1909) in his description of waxy maize from the Orient, they all tended to be gathered at one side of the culm and to hang over the developing tassel like a kind of spathe. While this character was more extreme in some varieties than in others, there was a marked tendency in that direction throughout the collection.

The arched and drooping spathe-like upper leaves were accented by the drooping and semi-included tassels. Tassel branches tended to be more slender than those of New World varieties, and in the more extreme varieties they hung down vertically until after the pollen was shed or even later. Though the tassel branches were long, the glumes were small. Because of the short upper internodes the tassels were never exserted from the upper leaves as pollen started to shed and many of them were not exserted even when fully mature.

For the ear the prevailing tendencies of the collection were to small cobs, prominent glumes, small, isodiametric kernels, and complete absence of row-pairing. The colors of their kernels were mostly a pale straw-yellow or a dull reddish-blue.

In their even green color, included tassels, slender culms, slender tassel branches, isodiametric kernels, straw-colored or dull blue kernels, these Assamese varieties resembled sorghum more closely than do New World varieties of maize, and one

variety even had a bluish-green bloom on its leaves rather similar to that which is so characteristic of certain varieties of sorghum.

Among the collections from the Naga a number of different sub-types could be distinguished. It seems unwise to dignify them with permanent names until we know more about the kinds of Oriental maize than we do at present. For the purposes of this discussion they may be provisionally designated as follows: I—Caribbean; II—Early Slender; III—Late Upright; IV—Early Upright; V—Late Sidewise; VI—Drooping Waxy. Some of their characteristics are shown in tabular form in table 1.

I—*Caribbean:* Types of maize fairly similar to those grown around the Caribbean basin are widely distributed in the Orient and were apparently introduced by the Spanish. They seem to be the prevailing type in the Philippines and in Guam and they or mixtures with them make up the bulk of the maize grown in Asia, particularly at lower elevations and along the coasts. In previous years I have grown collections from India, Guam, the Philippines, Sumatra, the valley of the Irrawady in Burma, and from China. One such variety was collected by Stonor (No. 17), though he commented as follows: "Evidently not quite a pure strain." The ear-to-row test of this collection showed more plant-to-plant variation than did Stonor's other collections among the Naga. In it the distinctive characters of the rest of the collection are less strongly developed. It grew more quickly, had more pronounced plant color and colored silks, it had coarse tassels, large ears with white kernels conspicuously capped with soft starch, and was the earliest of anything in the collection. It showed Assamese tendencies in its somewhat included tassel. It probably represents a fairly recent mixture between Assamese maize and one of those Caribbean types which were spread so widely around the world by the Spanish and the Portugese.

II—*Early Slender:* In its slender stem, long slender leaves, and most pronounced spathe at flowering time, this variety was very similar to VI. It differed in being the earliest of the distinctive varieties and in the morphology of the mature tassel. Although the tassel branches were completely pendent when they first appeared and even after they began to shed pollen they eventually stiffened to produce a tassel more like broom-corn than any other known variety of maize. The long, slender, wiry branches became stiffly distended when mature, and the small glumes (5–6 mm. long) were quite closely appressed. As in many of the varieties with short upper internodes, the auricle of the uppermost leaf was developed into a conspicuous tuft of long white hairs. Though to casual observation this variety seemed to be completely green, careful examination at the base of the plant showed a faint flush of color.

III—*Late Upright:* The leaves of this type were dark green, were held crisply erect until after the tassel appeared, and were twisted, usually one complete revolution and sometimes more. The plants had many short internodes and grew and

TABLE I

CHARACTERISTICS OF NAGA VARIETIES

Type	Stonor No.	C.I.T. No. 1948	Row Number	Kernel size in mm.	Kernel shape	Midcob width in mm.	Pith diam. in mm.	Base color	Tassel inclusion	Pendent tassel	Season	Chromosome knob number	Kernel color	Number of ears
I—Caribbean	17	1088	14	Large	Flat	26	11	+	Faint	Slight	Early		White	1
II—Early Slender	13	1084	14	Medium	Square	20	6	—	Strong	Medium	Early		Lt. yellow	1
III—Late Upright	5	1076	14	Small	Sphere	20	7	0	Strong	Strong	Early	4	Dull blue	4
	8	1079	20	Small	Sphere	22	11	0	Faint	Strong	Very late		Purplish	3
	9	1080	20	Small	Sphere	22	8				Very late		Dull blue	
	10	1081	16	Small	Sphere	19	7	0	Faint		Late	5–7	Dull blue	
	14	1085	14	Large	Subsphere	18	12	+			Late		Red-purple	
IV—Early Upright	6	1077	10	Very small	Sphere	18	3	+	Strong	Medium	Early		Red	4
V—Late Sidewise	11	1082	16	Small	Sphere	23	7	—	Strong		Very late	4–6	Lt. yellow	3
	12	1083	12	Small	Sphere	18	4	+	Strong		Very late	2	Or. yellow	4
	18	1089	14	Small	Sphere	19	4	+	Strong		Very late	4–5	Lt. yellow	4
VI—Drooping Waxy	16	1087	16	Small	Sphere	30	7	+	Strong	Strong	Mid-season		Ivory	2

developed slowly. The internode pattern of a typical plant is shown in fig. 1. The kernels are small, with a dull, purplish blue aleurone and are used as a popcorn (see Stonor's notes). Similar popcorns (as well as the actual popped kernels) have been received from correspondents in Siam. Stonor's different collections made among various Naga tribes were almost identical in growth type aside from one or two obviously out-crossed individuals. In their small kernels, upright twisted leaves, large number of ears, and pedicel and cob anatomy, this type resembles certain ancient popcorns of South America. Ears and popped kernels have been obtained from various graves and trash-heaps in coastal Peru and Chile (Anderson, 1947), and through the kindness of Dr. Paul Weatherwax a living example of such a popcorn was grown from one of Parodi's collections in Argentina. Since Ica times (the Ica preceded the more widely known Inca) these kinds of small-kernelled popcorns have been rare. At earlier times they were apparently the prevailing type along the coast of Peru and Chile and have been recovered from graves in the Argentine. A somewhat similar popcorn, of unknown origin, is sometimes grown in the United States in spite of its long season and small ears, because of its high quality. Though it has been extensively confused with the early-seasoned "Tom Thumb," its proper name is apparently "Ladyfinger," by which name it was first called in the United States at least a century ago (Emmons, 1849).

The tassels of Late Upright plants exhibited little or no condensation and from slight to pronounced multiplication (Cutler, 1946). The central spikes were prevailingly in whorls of three. Most of the plants grew four good ears with partly developed nubbins at lower nodes. Collection Nos. 5, 8, and 10 showed no base color (in other words they were like '*aa*' plants) and No. 14 which showed base color had larger and redder kernels and may well have been derived from a cross between a typical Late Upright and some other sort of maize. One cob of No. 8 was examined by Lenz (1948) and is figured by him, plate 38, fig. 5. It has the longest, slenderest pedicel ever reported for any variety of maize.

IV—*Early Upright:* This one collection (No. 6) was in every way like the Late Uprights except that it was earlier, had red seeds, and pronounced base color.

V—*Late Sidewise:* Both in Assam and in the United States this variety in the vegetative stage looks unlike anything previously reported for *Zea Mays.* The leaves and especially the culms are bluish-green with a distinct bloom. The tillers are practically horizontal during the first month or so of their development. On both tillers and main culm the internodes are very short, and even in the mature plants few ever exceed 10 cm. in length. Most agronomists, seeing the plants before they had tasseled out, would have wondered if they were some kind of sorghum. Base color varied from very faint to strong, and the leaves, even early in development, stood out at right angles to the culm. The ears were long and slender with small yellowish kernels. The large number of internodes (30 or more

per plant) was evidently not a response to a longer day length, since similar results were obtained in Shillong and since there were prop-roots at only one or two of the lower nodes.   (In tropical maize grown in the United States there may be prop-roots on 10 or more nodes as one result of the change in length of day.)

VI—*Drooping Waxy:* Up to flowering time this variety was much like II except for the later season and consequent higher number of leaves.   It had the same slender culm, slender green leaves, and, if possible, an even more highly developed spathe from within which the slender tassel branches drooped straight downward. Even at the end of the season, both in California and Assam, the tassel, though arching horizontally, was still quite pendent and much more extreme than any tendency of this sort in South American maize.   All the plants of this variety had waxy pollen, and an analysis of the kernels at the Northern Regional Laboratory at Peoria, Ill., bore out this diagnosis.   Stonor reported the young ears as being outstandingly sweet, and, like much of the waxy maize in the Orient, this is probably a specialized type used for green corn.   Waxy maize is cultivated in the vicinity of Chungking, China, as a table corn, and Kuleshov's monograph (1928) illustrates the same pendent tassel in waxy varieties from various parts of Asia.

To summarize: These remote Asiatic aborigines cultivate a number of exceptionally well-differentiated varieties of maize.   The following unusual characters typify one or more of these varieties:

Uniformly green leaves, culms, silks, and anthers.

Slender, pendent tassel branches.

Straw-yellow endosperm, dull bluish-red aleurone.

Small, isodiametrical kernels.

Many short internodes, lack of vegetative vigor.

Upright, twisted tassel branches, short silks.

Tassel included in upper leaves at flowering time; leaves immediately below it falsely monostichous, forming a sort of spathe; tassel not completely exserted even when mature.

Waxy pollen and endosperm.

As we shall demonstrate below, this complex of characteristics is widely distributed in the back corners of Asia.   It would be of primary significance to know where it is most closely approached in the New World.   Certainly nothing like it is known from Mexico, Guatemala, or other parts of Central America.   The only United States variety showing any of these characteristics is "Ladyfinger" popcorn, a variety of unknown origin which has been in this country for at least a century (Emmons, 1849).

In South America this complex of characters is rare, and most of the collections and published descriptions demonstrate radically different types of maize throughout that continent.   However, a popcorn collected at Chiu Chiu, a remote oasis in

the Atacama desert of northern Chile, by Carl and Jonathan Sauer, has a number of features in common with these Oriental varieties (Anderson, 1943). Furthermore, as mentioned above, an indigenous popcorn collected in Argentina by Parodi, shows many of these same characters. A photograph by Jonathan Sauer of still another variety from Chiu Chiu, Chile, shows the multiple ears, the short silks, and the short upper internodes of the oriental varieties. In a collection of native corns from the Bolivian edge of the eastern lowlands, kindly turned over to me by Dr. H. C. Cutler, there were several plants which had the green plant color, pendent tassels, multiple ears, and spathe-like upper leaves of the Oriental varieties. Dr. F. C. Brieger informs me that he noted some of these same characteristics in other collections from these valleys. Insofar as one can judge from characters of the mature ear, a fairly similar set of varieties was once common on the west coast of South America. All the collections of early prehistoric maize from that area (and the museum material is so rich that it has not yet been possible to measure and record all of them) shows a small-cobbed variety with isodiametrical kernels, much of it apparently a popcorn, since the prehistorically popped kernels are known from a number of sites. This type, uniform in the lower archaeological levels, became gradually more variable and was supplanted by larger-kernelled types similar to modern Andean maize, when the Icas extended their influence down to the coast in times preceding the Inca domination.

In the Orient, on the other hand, similar varieties are widely, though very spottily, distributed. They are associated with the most primitive cultures in southeastern Asia, principally with the Tibeto-Burmans and allied peoples. In 1909 G. N. Collins published an exhaustive account of a variety of maize with a waxy endosperm which had been collected in China. In 1920 the same author, in a short communication, reported that waxy maize and other curious varieties had been obtained from the hill tribes of Upper Burma. Collins' description of waxy maize would apply equally well to most of the Naga varieties:

> While in only about 25 per cent of the plants were the upper leaf blades completely monostichous, all of them showed a tendency in this direction. This one-ranked appearance is brought about by a twisting of the leaf sheaths, the actual insertion of the leaves being opposite as in all grasses. In addition to the unusual position of the leaves the blades of the upper nodes were erect instead of spreading or dropping as in other varieties . . . . The internodes on the upper part of the plant were also much shortened, so that the tassel was not carried up, as in other varieties (loc. cit., p. 8).

His description (loc. cit., p. 13) of the aleurone color is also applicable to many of the Naga collections:

> The color of the aleurone layer was distinct from anything that has been observed in other varieties. It varied greatly in intensity. In rare cases it approached the bluish black of our common "black" varieties, but for the most part varied from a dull ruby to maroon. The color was usually confined to the top of the seed, fading out toward the base.

Under Vavilov the Russians made a comprehensive survey of Oriental maize which was reported upon by Kuleshov in 1928. It is extensively illustrated and accompanied by a summary in English (pp. 371–374). It demonstrates that

varieties similar to those described from the Naga country are widespread in central Asia from Persia and Turkestan to Tibet and Siberia. Figure 6, a variety from Persia, shows the characteristic short silks described by Collins and fig. 11 (3–6) shows tassels covered by a spathe of leaves in Persian and Turkestan varieties. Extremely pendent tassels from a number of points are described and illustrated. On pages 373–374 Kuleshov summarizes his morphological evidence.

> Asiatic maize shows a series of characters which are either unknown or very rare in American[1] maize. These characters manifest themselves in connection with a definite area, sometimes a very large one. Thus the waxy endosperm is spread from 5 to 45° North lat.; the short plant habit is peculiar to the vast expanse of Central Asia; panicles covered by the upper leaves and silks hiding in the axil of the leaf are met with in specimens from eastern Asia to Transcaucasia, etc.

The question of the introduction of maize into the Orient was gone into exhaustively by B. Laufer (1909). He came unequivocally to the conclusion that it was not introduced into China from the coast like other American crops but spread overland via Tibet. He was an accomplished linguist and bibliographer but without botanical training and had had to take the word of the botanists of his day that maize in the Orient was morphologically not different from maize in the New World. With this as a premise he could have come only to the conclusion he finally reached: that maize somehow got to Indian ports at an early post-Columbian date and spread overland via various primitive peoples to China. He quotes no botanical authorities for the morphological equivalance of Asiatic and New World maize, merely stating (footnote p. 224) his premise "If maize were indigenous to Asia, we should expect to find there either a wild form, from which the cultivated species are derived, or the Asiatic species to be differentiated from that of America, neither of which is found." Had the botanists of his day studied Oriental maize in even a cursory fashion they would have found that Asiatic maize is indeed "differentiated from that of America," most particularly in that very area between China and India which Laufer decided must have been the route by which the crop eventually reached China. His monograph is a mine of information as to the frequency of maize among these various primitive peoples and the role it plays in their economy:

> In the remarkable culture of the small mountainous tribe of the Lepcha in Sikkim, a people closely related in language to the Tibetans, maize plays a significant role, and it is surprising to note what a rich terminology they have developed with regard to its economy. There are four words for maize, two for the flowers of maize; and no less than eighteen varieties, by means of attributes are distinguished. Further the head of maize has several names according to its growth. There is a special expression for the young head when first appearing, for the head when seed commences to appear, when the grain begins to get a little larger, when the grain begins to get a little firm, when the grain has acquired firmness and for the head when ripe! [loc. cit., p. 242] . . . . It is interesting to note that among all the so-called aboriginal tribes of western and southern China, maize forms the favorite and principal food and is more highly appreciated by these tribes than by the Chinese. [loc. cit., p. 244].

---

[1] It should be emphasized that Kuleshov (1930) produced a monograph on the collections of maize made by Vavilov and his collaborators in Central and South America and was probably as familiar with the morphology of New World maize, as a whole, as any other investigator.

Laufer quotes (loc. cit., p. 245) B. C. Henry who says that in China maize "is now very extensively cultivated by the Chinese, but especially by the aboriginal peoples, among whom it seems to be almost as great a favorite as among the American Indians. It forms a main portion of the sustenance of both the aborigines in the north-western corner of Kwantung and of those in Hainan."

Through the courtesy of Dr. Ian Khambanonda it was possible to import a sample of a popcorn from Siam. It has violet-blue kernels similar to those of the Assamese varieties received from Stonor. Dr. T. W. Whitaker kindly grew a few plants of it for me at the U. S. Dept. Agr. Vegetable Breeding Laboratory at La Jolla, California. In its long season, upright leaves, slender tassel branches, short internodes, and large number of ears it closely resembled the Assamese popcorns. Popped kernels were also forwarded from Siam but Dr. Khambanonda was unable to supply very much detailed information because maize in Siam is grown principally by the aboriginal hill-tribes, seldom by the Siamese.

To summarize: A number of distinctive maize varieties are grown in the remotest parts of southeastern Asia, particularly by the aborigines of various hill tribes. Without exception it is more common among these primitive folk than among their civilized neighbors. In China it is more common and more appreciated among the aboriginal tribes of western and southern China than by the Chinese (Laufer, loc. cit.). Dr. Khambanonda testifies to its almost exclusive cultivation in Siam by the aborigines. Interviews with Ko Ko Lay, now an exchange scholar from Burma, have produced similar testimony for Burma. Dr. Pierre Larroque, the former maize breeder for Indo-China, tells me that among the primitive Meo, ethnologically related to the Tibetans, it is very commonly grown and that on the Yunnan border it seems almost to run wild. Mr. Stonor, the author of the first section of this paper, having been transferred to New Guinea, informs me that although it is either unknown or very recent along the coast, it is found among the primitive peoples of the interior. Its importance among the Lepcha of Sikkim and the aboriginal Li of the Island of Hainan has already been alluded to.

That maize could in post-Columbian times have spread to each of these various hinterlands without entering into the economies of the more civilized people who would have handed it on almost passes belief. Had it spread only to the Naga, one would have wondered what special circumstances caused its adoption by a people so remote that one ethnographer describes them as having lived for thousands of years "in these hills, as on some happy island, almost untouched by the waves of civilization which from time to time have surged through the plains of Assam and the valleys of Upper Burma. Ancient cultures which were once spread over great parts of southeastern Asia and which in most countries had finally to give way before the higher Indian and Chinese civilizations have been preserved here in a comparatively untouched form, and allow us to observe with our own eyes, early types

of human culture" (von Fürer-Haimendorf, 1939). Furthermore, when we examine the maize of these people it is not the dominant world crop of Central and North America. It is relatively unproductive and with less vigor than other known types of maize. To believe that in post-Columbian times maize could have penetrated not only to the Naga but to the hill tribes of Upper Burma, and of Siam, to the Lolo in central Asia, to the aborigines of Hainan, to the hill peoples of Sikkim, and to the interior of New Guinea, in each case passing over the more civilized peoples along the coast is beyond credulity. To have these conservative people somehow learning to use maize as a popcorn and as a green corn and as a cereal for brewing, to have them growing types of maize which are similar to each other yet rare or unknown in the New World puts the burden of proof on any one who would ascribe all this development to separate post-Columbian acquisitions.

It seems more likely that there have been at least two major movements of maize in Asia. The latter in early post-Columbian times brought what is essentially a Caribbean type of maize to the Philippines and to many countries actively colonized by the Europeans. Back in the hills, however, are much more primitive types, unaggressive, not particularly productive, grown by conservative people. If one asks why they did not spread more the answer is that they did spread in Asia from Persia to Sumatra and New Guinea, which is virtually as far as the Asiatic *Sorghum* (which was their companion crop) has been carried.

The general evidence for the main kinds of maize in South America and in southeast Asia is crudely and diagramatically summarized in fig. 2. The letters *A*, *B*, and *C* represent three of the major races which make up *Zea Mays*. Letters within parentheses indicate that a particular type is present but is relatively uncommon. Each of these major races has a core of morphological characters in common in spite of great variation from variety to variety within the race (Anderson and Cutler, 1942). *A* represents the small-kernelled types we have just been describing and mixtures with them. In South America they are found today either as rare native popcorns or as one of various primitive tendencies in the highly heterozygous maize of the eastern river basins (Cutler, 1946). In Asia they are practically confined to hill areas and in the most isolated are the only type. In western South America, where we have stratigraphic archaeological evidence, we know that race *A* was for centuries the only type of maize. *B*, in fig. 2, represents the distinctive large-seeded frequently large-cobbed types of the Andean region, which are practically exclusive at higher altitudes, which have dominated (at least in mixtures) the west coast ever since prehistoric times (late Ica) and which are one of the elements in the maize of the Amazon basin. Such types are apparently unknown in Asia, a most significant fact. *C* stands for the widely adaptable types of the Caribbean basin which spread so rapidly and extensively around the world in post-Columbian times.

This diagram is factual and though some of these facts are matters of judgment; with other types of maize it has already proved possible to make objective records of such racial differences (Anderson, 1944; Brown and Anderson, 1947; and Anderson, 1947), thus taking such questions out of the realm of acrimonious quibbling. The interpretation of these facts is quite another matter. The facts are in themselves fantastic; any satisfying hypothesis must border on the miraculous. One fact seems to be clear. Race C, which we know to be archaeologically post-Columbian in South America, was widely spread in post-Columbian times. If we therefore remove C from consideration, the problem to be solved is how could race A get to a number of isolated hill areas in Asia without anywhere leaving a very definite record along the coast of Asia? If, for the sake of argument, we grant that it might somehow have spread there from the Upper Amazon in post-Columbian time, who brought it and how? Was there somewhere in the New World a reservoir of various A varieties which has since disappeared? Could all the A varieties in Asia have differentiated themselves in all these backward areas into a set of unique but similar varieties under the stimulus of a new environment? These are possibilities but they certainly seem fantastic.

If we admit (with a growing minority of archaeologists) the possibility of trans-Pacific contact in very early pre-Columbian times, then race A might have crossed the Pacific at an early date when maize was still an unaggressive little popcorn, to be carried across the Pacific again when the dominant world crop which we now know had been developed in the New World. As to which way maize made its first crossing, whether from Asia to the New World, or *vice versa*, the facts of fig. 2 do not even suggest an hypothesis. From the generally accepted facts as to the relationships of maize a good case could be made out for either Asia
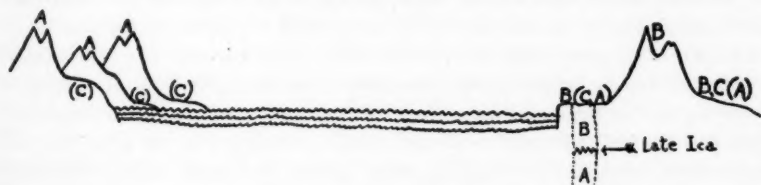

Fig. 2. Distribution of the major races of maize in South America and in Asia. Very diagrammatic, A, B, and C represent three of the main kinds of maize, each consisting of various sub-races and innumerable varieties. Though these races may intermingle, each has its own core of correlated tendencies: Race A, archaeological and Asiatic—small ears, large glumes, subspherical seeds, short internodes, drooping and included tassel, green plant color; Race B, Andean—large kernels, pineapple-shaped ears, large cobs, strong plant color; Race C, tripsacoid—long ears, stiff tassel, bony cob. Letters in parentheses indicate areas where a particular race is known only in mixtures with other races. In the Orient race C is represented in "Caribbean Flints" a mixture of C and other races. Asia is diagrammed to the left of the figure, South America to the right, with the Pacific in between. For western South America there is extensive archaeological evidence, some of it stratigraphic, which allows us to establish a sequence of maize types from A to B.

or the New World as a primary center. There can be no doubt that the New World was certainly the secondary center, or rather a whole set of secondary centers.

The physical possibilities of transfer by the early Polynesians are much more likely than most botanists are aware. These early people were skilled navigators who could deliberately set out for Hawaii from Samoa and arrive at Hawaii. Furthermore, they were skilled cultivators who carried vegetatively propagated varieties of various crops to many of the islands of the Pacific (Buck, 1938). Getting the improved taro and bread-fruit to Hawaii (which they are known to have done) would have called for more skill as navigators and cultivators than to have taken maize from New Guinea to Peru.

Nor would maize have been exceptional among cultivated plants had it been taken across the Pacific. It is known that the gourd crossed the Pacific in very early pre-Columbian times and it is admitted by most authorities that the cultivated sweet-potato originated in the New World but spread in pre-Columbian times to Polynesia and even as far as New Zealand. The sword bean *(Canavalia)*, widely cultivated throughout the Pacific and always considered to be of Old World origin, is now known from prehistoric sites along the coasts of both South America and Mexico.

The hypothesis here suggested as to the origin and developments of maize is paralleled almost exactly by the conclusions concerning cotton reached after long cooperative research by the British cotton experts (Hutchinson, Silow & Stephens, 1947). In the case of cotton, polyploidy operated to keep certain mixtures of old and New World germ-plasm from losing their identity in the mixture, thus making the story quicker to untangle and more difficult to controvert.

For many minor domesticated plants, the rather complete neglect of cultivated plants and weeds by taxonomists leaves any general discussion of the problem at the stage of mere guesswork. Neither the cotton story nor that of maize could be put together until a beginning had been made at the fiendishly difficult problem of classifying and cataloguing their various cultivated varieties. Both Amaranths and Chenopodiums are cultivated by the hill peoples of Asia and of the New World as cereal crops, pot-herbs, ornamentals, magic plants, and food colors. Not until these groups have been meticulously collected and monographed (the cultivated strains, the weeds, and the genuinely wild entities) can we be in a position to discuss the evidence. Similar careful studies are needed of the various strains of *Bixa Orellana*, of Job's tears *(Coix)*, of *Pachyrhizus*, all of which are widely distributed in both the Old World and the New. There is little really critical taxonomic evidence on origin and diffusion for any of these groups at present. It is disappointing to find, half-way through the twentieth century, that our botanical evidence is not yet at a stage where such fundamental questions can be authoritatively discussed. For the plants most directly associated with man, the cultivated plants

and weeds, aside from a few collections by such pioneers as Ames, L. H. Bailey, and Merrill, we do not have the specimens let alone the critical studies. The average botanical collector is so intrigued by cloud forests and river jungles that he does not even think about the more difficult problems posed by the vegetation of dump-heaps, clearings, and cultivated fields.

For maize itself, two facts suggest how complicated a story may be involved: (1). The relationship of *Sorghum*, Assamese maize, and prehistoric North American maize. Whatever the explanation, it is clear that the maize of Assam is more like *Sorghum* in a number of different ways than is any other modern maize as yet examined in detail. Whatever the explanation, it is also clear that the earliest prehistoric maize cob described from Bat Cave, New Mexico, by Mangelsdorf and Smith (1949) is even more *Sorghum*-like in the details of its inflorescence, while cobs from the upper layers of the same cave are as radically un-*Sorghum*-like as it is possible for maize inflorescences to be. It may be that maize and *Sorghum* have had a parallel evolution in the Orient under the stimulus of a similar set of environments. It may be that they are related in some way; it is known that they have the same chromosome number. Whatever the explanation, the whole story must be a complicated one. (2). Much of the maize of Central and North America has knobs on its chromosomes, a character which Mangelsdorf and Reeves ascribed (1939) to introgression from *Tripsacum*, a New World grass. Much of the maize of South America is knobless. The maize of Assam has only a few knobs but they are frequently quite large and they tend to occur at positions and in combinations which are either rare or unknown in New World maize. Here again a complicated history of exchange and evolution is suggested.

Only one thing is certain. We must have extensive and critical collections of Oriental maize if we are to understand *Zea Mays* and utilize it most effectively. We need this information for practical and theoretical purposes. Kuleshov (loc. cit.) describes and illustrates dwarf, drought-resistant types from Persia. Larroque tells (personal communication) of a small-grained sort raised in Indo-China for chicken feed which germinates effectively in the soaking wet soil of rice paddies. More important and far-reaching is the need for such collections if we are to understand the history of maize. Along with *Drosophila* and *Neurospora*, the science of Genetics is built on work with *Zea Mays*. The brilliant work of Stadler and of McClintock, for instance, might have quite different implications for the fundamental nature of evolution or for the protein chemistry of the germ-plasm, depending upon the actual history of the germ-plasm which they have been using, the germ-plasm of *Zea Mays*. Certainly we cannot even discuss the probable history of *Zea Mays* in an intelligent fashion until we have at least an approximate notion of what varieties of maize are being grown by the Lolo in central Asia, by the hill tribes of Burma, Siam, and Indo-China, by the aboriginal remnant in Hainan and Formosa, and in the isolated interior of New Guinea.

GENERAL SUMMARY

Part I:—

1. The various hill tribes of Assam and neighboring regions are enumerated and their relationships to each other and to outside peoples are briefly described. In general, these tribal peoples grow their own food, weave their own clothing, and regulate their own affairs by tribal law. They have no writing and their religion is animistic.

2. The varieties and uses of maize are enumerated tribe by tribe. It is used for human food, particularly when immature (i.e., as "green corn"), for beer-making, as popcorn, and for pig-feeding. Its importance varies from tribe to tribe but, along with the cereal forms of Job's-tears *(Coix)* and millet *(Sorghum)*, it is traditionally one of the ancient foods of the region.

3. It is usually grown in lines or patches or as single plants among other cereal crops. In spite of this practice, the varieties are kept remarkably pure, even when five or six distinct types are grown by a single village.

4. The wide distribution in the area, the traditions and positive statements of the peoples themselves, the existence of tribal names, and the place of maize in their religions all point to a long history in this region, going back for centuries at least and most probably antedating rice culture there.

Part II:—

1. The assembling of all the evidence on the morphology of these Assamese varieties was a complicated affair, because their growing season is long and because the importation of maize from southeastern Asia is necessarily restricted[1]. They were collected directly from the Naga and grown in duplicate in Assam and California. A set of the original ears was photographed on the ear in London, and plants from ear-to-row tests were photographed in California and in Assam. Pachytene smears were made of many of the cultures, and a few of the original cobs were studied in celloidin section by Lenz.

2. There are considerable differences between the Assamese varieties (most of which are remarkably uniform within the variety). As a whole they tend to have: slight or no plant color, many short internodes, semi-included tassels, spathe-like upper leaves, pendent tassel branches, several small ears, long slender leaves, short silks, dull aleurone colors, small subspherical kernels. They are outstanding, both in Assam and in this country, for their lack of vigor.

3. This complex of characters is unknown in Mexico and Central America. In South America it is approached only in mixtures from the eastern rivers and in certain primitive popcorns. In prehistoric times, varieties with similar cobs and kernels were the only type of maize along the west coast of South America for a very long period.

---

[1] Due to the presence of two of the world's worst maize diseases in this area, in itself a significant fact.

4. The distribution of these and similar varieties in the Orient is reviewed. They are widely though spottily distributed from Persia and Turkestan to Tibet and the Island of Hainan, nearly always among primitive and conservative peoples.

5. It is concluded that there have been at least two major movements of maize in Asia. The later one, in early post-Columbian times, brought what is essentially a Caribbean type of maize to the Philippines and to many of the countries actively colonized by the Europeans. Back in the hills, however, are more primitive types whose progenitors must have crossed the Pacific in pre-Columbian times, though in which direction (or directions) the evidence does not indicate.

6. The possibility of trans-Pacific transfer of a primitive and unaggressive race of maize by early Polynesians is discussed. It is shown to parallel the conclusions reached by the most recent workers on cotton. For the study of such problems, the imperative need of more critical taxonomic evidence on cultivated plants and weeds is discussed and illustrated by examples.

7. It is concluded that maize has had a long and complicated history. As a dominant crop it certainly developed in the New World. As a primitive, relatively unproductive crop, utilized for brewing, for popping, and for green corn, it is almost universal among the primitive peoples of central and southeastern Asia. Presumably it must either have originated in Asia or have been taken there in pre-Columbian times. Before we can discuss the history and origin of maize intelligently we shall need an approximate survey of the kinds of maize being grown by these peoples.

BIBLIOGRAPHY

Anderson, Edgar (1943). A variety of maize from the Río Loa. Ann. Mo. Bot. Gard. 30:469–474.
————, (1944). Maíz reventador. Ibid. 31:301–312.
————, (1946). Maize in Mexico. Ibid. 33:147–247.
————, (1947). Corn before Columbus. 24 pp. Des Moines, Ia.
————, and William L. Brown (1947). The northern flint corns. Ann. Mo. Bot. Gard. 34:1–22. pl. 1–6.
————, and H. C. Cutler (1942). Races of Zea Mays. I. Their recognition and classification. Ibid. 29:69–86.
Buck, Peter H. (1938). Vikings of the Sunrise. New York.
Collins, G. N. (1909). A new type of Indian corn from China. U. S. Dept. Agr. Bur. Plant Ind. Bull. 161:1–30, pl. 1–2.
————, (1920). Waxy maize from Upper Burma. Science, N. S. 52:48–51.
Cutler, Hugh C. (1946). Races of maize in South America. Bot. Mus. Leafl. Harv. Univ. 12:257–291.
Emmons, Ebenezer (1849). Agriculture of New York 2:263–265. Nat. Hist. N. Y. Pt. V, Vol. 2.
Von Fürer-Haimendorf, Cristoph. (1939). The Naked Nagas. 243 pp. London.
Hutchinson, J. B., R. A. Silow, and S. G. Stephens (1947). The evolution of Gossypium. 160 pp. Oxford Univ. Press.
Kuleshov, N. N. (1928). Some peculiarities in the maize of Asia. Bull. Appl. Bot. and Pl. Breed. 19:325–374.
————, (1929). The geographical distribution of the varietal diversity of maize in the world. Ibid. 20:506–509.
————, (1930). The maize of Mexico, Guatemala, Cuba, Panama, and Colombia. Ibid. Suppl. 47:492–504.
Laufer, B. (1907). The introduction of maize into eastern Asia. Cong. Int. des Americanistes. pp. 223–253. Quebec.

Lenz, L. W. (1948). Comparative histology of the female inflorescence of *Zea Mays* L. Ann. Mo. Bot. Gard. **35**:353–376.

Mangelsdorf, Paul C., and R. G. Reeves (1939). The origin of Indian corn and its relatives. Texas Agr. Exp. Sta. Bull. 574.

————, and C. Earl Smith, Jr. (1949). New archaeological evidence on evolution in maize. Bot. Mus. Leafl. Harv. Univ. **13**:213–247.

Merrill, E. D. (1941). Man's influence on the vegetation of Polynesia with special reference to introduced species. Proc. Sixth Pacific Cong. **4**:629–639.

EXPLANATION OF PLATE

PLATE 18

Fig. 1.   Monba tribe.   Threshing maize, Dirang village.   (November, 1946).

Fig. 2.   Monba tribe.   Maize stacked for ripening, Pakung village.   (November, 1948).

1

2
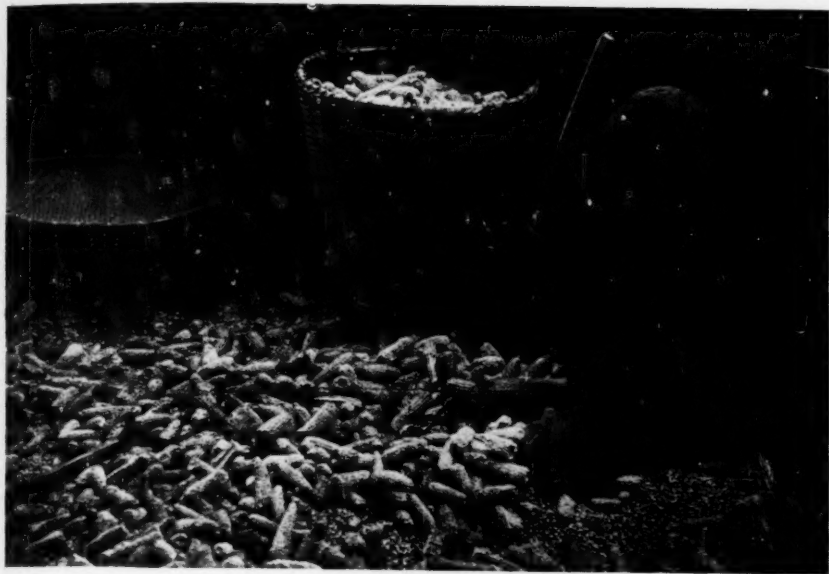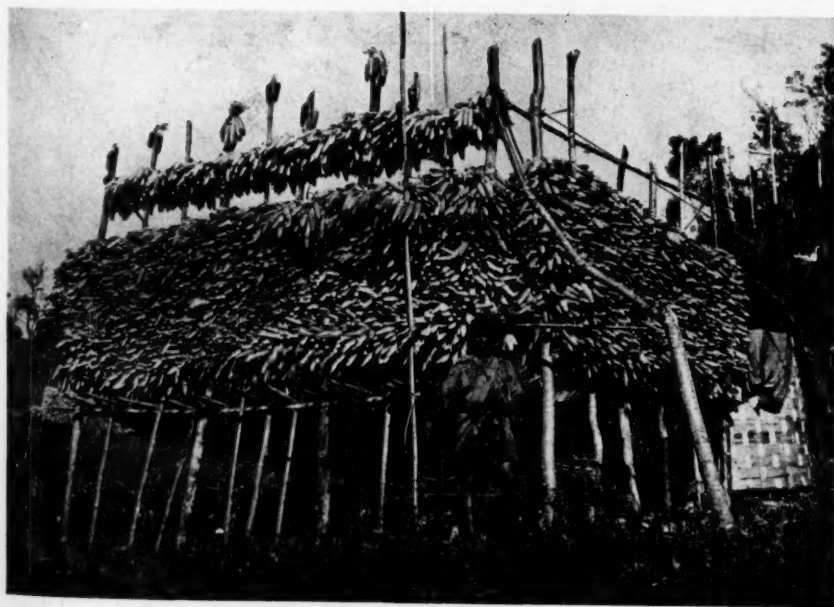
STONOR & ANDERSON—MAIZE OF ASSAM

EXPLANATION OF PLATE

PLATE 19

Fig. 1.   Eastern Dafla tripe. Carrying in the maize from the fields. (November, 1946).

Fig. 2.   Lhota Naga tribe. Corner of a "jhum" field, with lines of maize growing among the rice. (May, 1947).

1

2

STONOR & ANDERSON—MAIZE OF ASSAM

400   ANNALS OF THE MISSOURI BOTANICAL GARDEN

EXPLANATION OF PLATE

PLATE 20

Three views of Stonor No. 13 (Early Slender). Scale indicated by the lines in the background which were originally spaced at 50 cms. Below: habit of plant when tassel began to shed pollen. Note the "spathe" of upper leaves which is directed towards the camera. Upper left: the same, viewed from the side. Upper right: close-up of tassel after pollen shedding was complete. Note proximity of upper leaf to base of tassel. Photographs courtesy of California Institute of Technology.
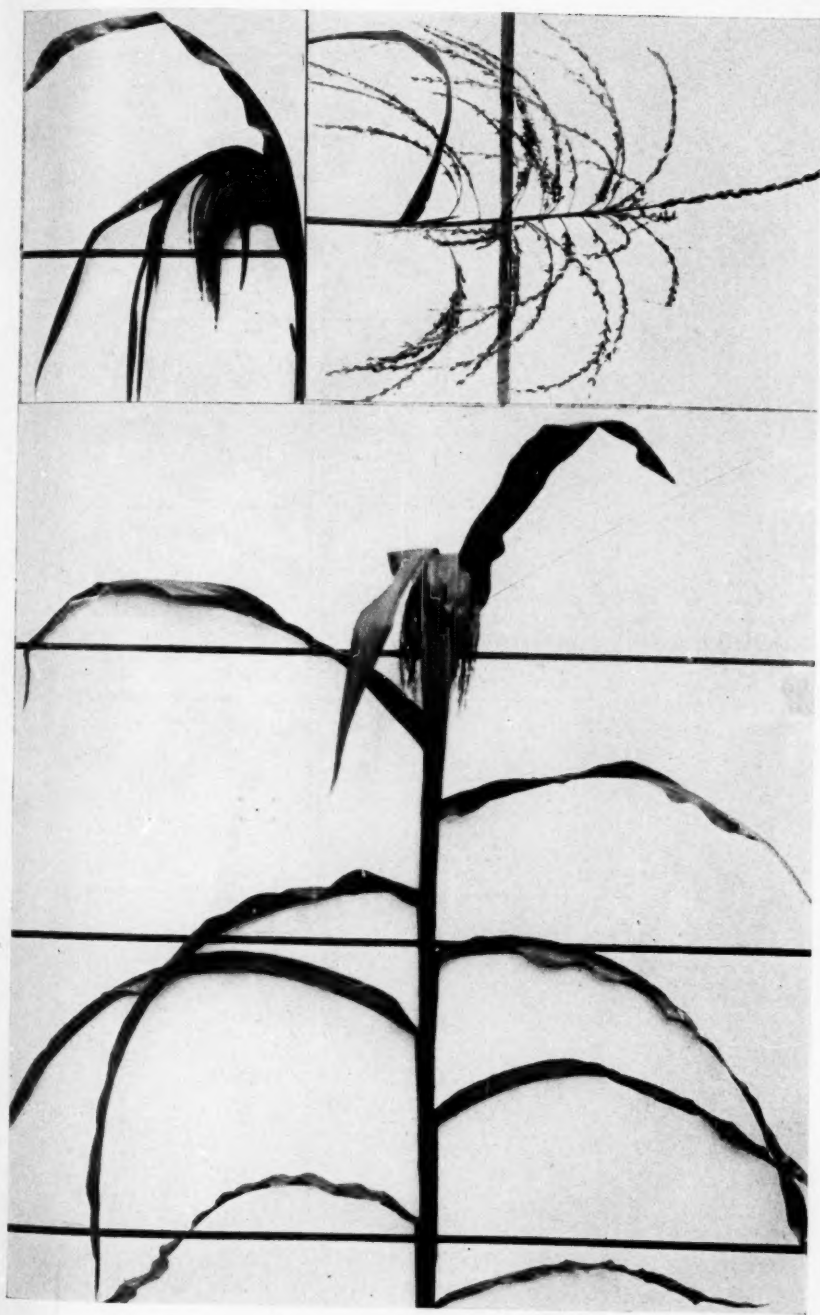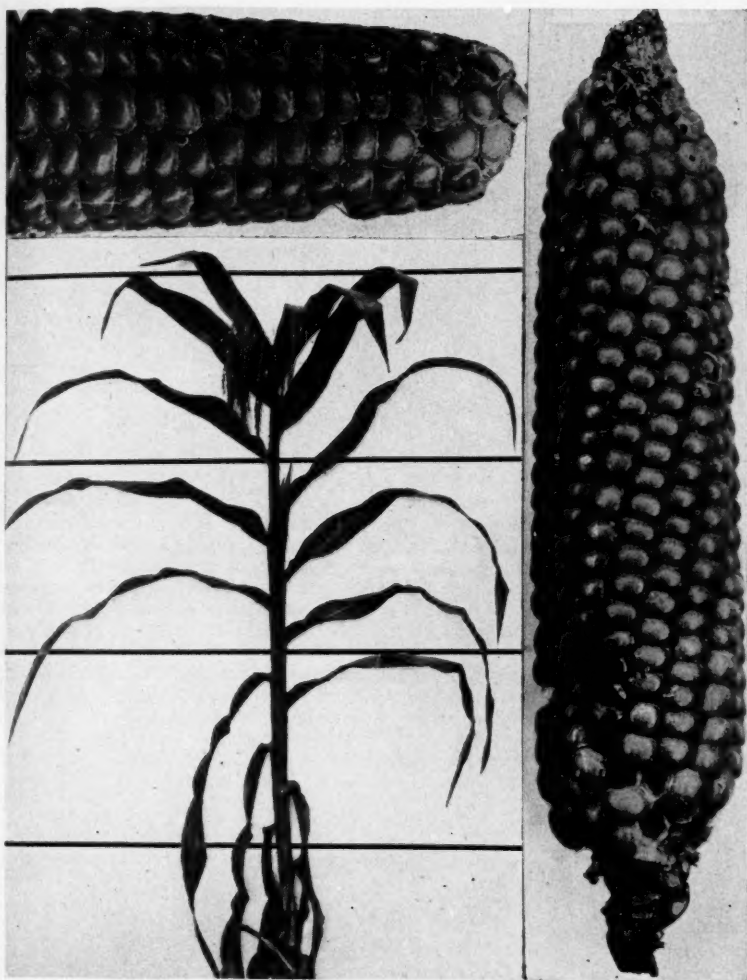
STONOR & ANDERSON—MAIZE OF ASSAM

EXPLANATION OF PLATE

PLATE 21

Lower left: habit of Stonor No. 16 (Drooping Waxy). Scale indicated by the lines in the background, originally spaced at 50 cms. Note clustering of upper leaves due to short internodes. Tassel had been shedding for some time and was nearly mature when the photograph was taken. Photograph courtesy of California Institute of Technology. Right: ear of Stonor No. 18 (Late Sidewise). Approximately natural size. Above: portion of ear No. 13, approximately natural size. Photographs of ears, courtesy of Royal Botanic Gardens, Kew, England.
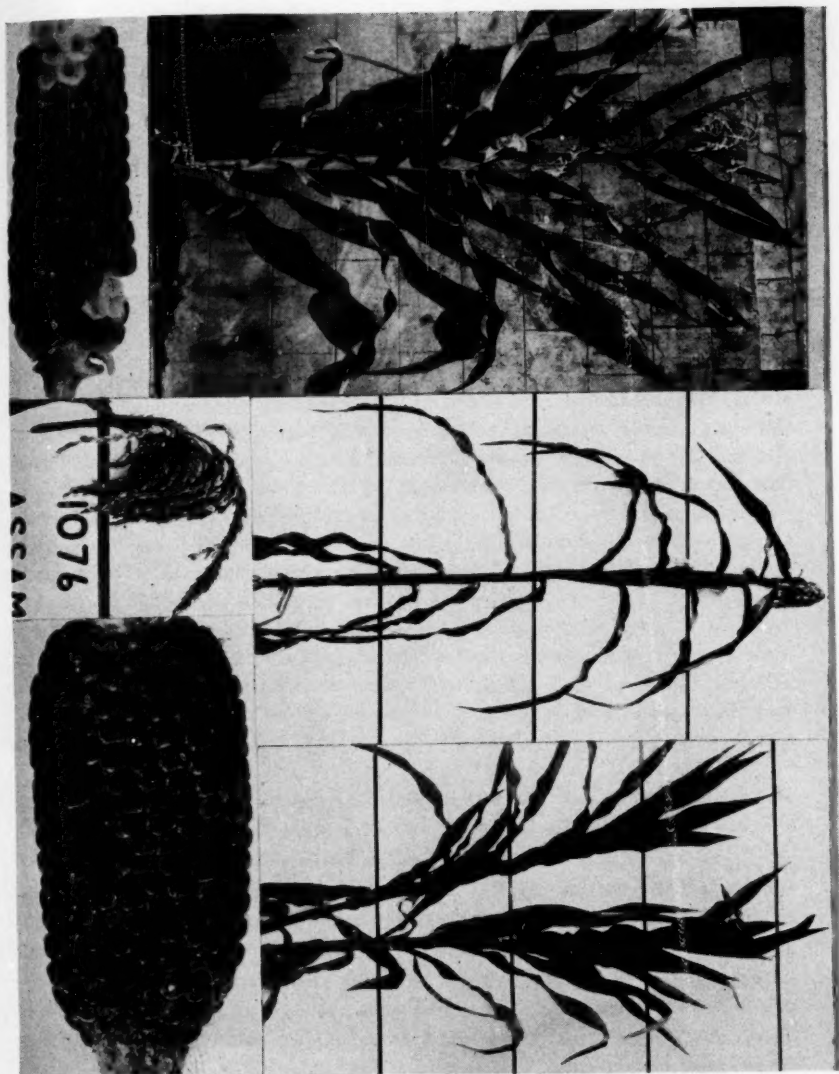
STONOR & ANDERSON—MAIZE OF ASSAM

EXPLANATION OF PLATE

PLATE 22

Ears and plates of Late Upright and Early Upright. Upper left (with stone back-ground), photograph of Stonor No. 8, taken in Shillong, Assam. Note erect and ribbed leaves, still slightly twisted, and that ears scarcely extend from the axils of the leaves. Center above: Stonor No. 5, photographed at a slightly later stage just as the silks were beginning to wither and after all the pollen had been shed. Note that tassel is not com-pletely exserted from upper leaves and that mature ears scarcely exceed their subtending sheaths. Center below, tassel of same plant with its uppermost leaf. Upper right: Stonor No. 6, habit just as tassel was beginning to shed pollen. Note tassel practically hidden by the upper leaves, which are twisted, upright, and ribbed. Scale in this and previous two figures indicated by lines which were originally spaced at 50 cms. Photographs courtesy of the California Institute of Technology. Lower right: ear of Stonor No. 8; lower left: ear of Stonor No. 6, both a little less than natural size. These two ears are almost identical with the popcorns found in early prehistoric graves in coastal Peru (Paracas, Cañete, etc.). Photographs of ears courtesy of Royal Botanic Gardens, Kew, England.